RESOURCE CAPTURE AND USE IN SEMI-ARID OVERSTOREY AGROFORESTRY SYSTEMS

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ABSTRACT

The work reported here aimed to provide a comprehensive database of core information to support the development and validation of process-based models of resource capture and growth in semi-arid overstorey agroforestry systems. Intensive field studies were carried out in Kenya over a 30 month period and the results obtained were combined with data from a previous project to produce a dataset spanning a 4.5 year period. This dataset was then used to verify output from the HyPAR model.

Allometric procedures developed from the pipe model theory (Lott *et al.*, 1998) were used to estimate tree growth non-destructively throughout the observation period. Significant differences in tree size between the sole (Td) and dispersed agroforestry (CTd) treatments were established during the first 130 days after planting, probably because of competition with the associated crops. The above-ground biomass and trunk length and taper characteristics of the CTd trees remained inferior to those of Td trees throughout the observation period, seriously undermining the economic potential of this agroforestry system. The biomass and grain yield of CTd understorey crops were similar to the corresponding sole crops during the first three seasons, but were negligible in three of the final four seasons, with maize yields reaching 50 % of the equivalent sole crop values only when seasonal rainfall was well above average. This observation suggests that water availability was the primary limitation for CTd maize during the final seasons of the trial, a conclusion supported by the superior performance of maize grown under net enclosures which simulated tree shade in the absence of below-ground competition. Cowpea and maize were grown concurrently in two seasons to examine the impact of grevillea on C4 and C3 crops with contrasting responses to shade; biomass and grain yield were less affected in cowpea than in maize.

The tree canopy in the dispersed agroforestry (CTd) treatment reduced the daily mean quantity of radiation incident upon the understorey crops by c. 30 % during the final four growing seasons, although the discontinuous nature of the tree canopy caused substantial local variation in shading intensity. Seasonal mean fractional interception was greater for the combined canopies of the CTd treatment when soil moisture status

was relatively high than for either of the sole canopies, suggesting the occurrence of spatial complementarity.

Tree shade had a substantial moderating influence on meristem temperature since the mean diurnal temperature range was reduced from a maximum of 20 °C in sole maize to 13 °C under the trees, and maximum meristem temperature was decreased by up to 6 °C relative to sole maize. However, the non-uniform shading provided by the trees caused substantial spatial variation in thermal time accumulation and hence crop development.

Grevillea continued to grow during dry seasons and was therefore able to capture off-season rainfall which might otherwise have been lost from productive use. In addition, adaptation of heat balance gauges for use on grevillea roots (Lott *et al.*, 1996) showed that substantial quantities of water could be extracted from deep-seated reserves below the crop rooting zone during dry periods, indicating the potential for spatial and temporal complementarity. However, transpiration by grevillea greatly exceeded rainfall during the dry season, rapidly depleting residual water supplies which might otherwise have been available for crop growth. In addition, approximately two thirds of the water used by the trees during cropping seasons was extracted from the soil surface horizons by lateral roots at distances of up to 2 m from the trunk. Thus, the potential for above and below-ground complementarity may be seriously undermined by the extensive capture of water by tree roots from the crop rooting zone.

Comparison of output from the HyPAR model against the observed results provided information pertinent to future model development. The model proved to be insufficiently flexible for end-users wishing to simulate the growth of different crops during the same simulation cycle, or to use model output to aid management decisions such as the timing of pruning. The allometric procedures used by the model to estimate canopy size from trunk diameter at breast height also proved incapable of accounting for reductions in canopy size resulting from pruning. Estimates of tree height are rounded to the nearest metre within the model, representing a potentially serious loss of resolution when annual increments often do not exceed 2 m. In addition, the numerous parameters required by the model would force most end-users to rely heavily on published information, potentially undermining the reliability of simulations.

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CHAPTER 1
INTRODUCTION

1.1 NATURAL AND MANAGED SYSTEMS IN SEMI-ARID ENVIRONMENTS; THE ROLE OF AGROFORESTRY

1.1.1 The semi-arid environment

The productivity of agricultural systems in semi-arid environments is often severely constrained by the prevailing environmental conditions (Monteith and Elston, 1993). Indeed the generally accepted definition of 'semi-arid' is based on the climatic conditions which affect vegetation growth (FAO, 1994). Rainfall is low (400-1000 mm; McIntyre, 1993), unevenly distributed (confined to a 2.5-6 month period) and varies greatly in intensity (20-60 mm h^{-1}; Monteith and Virmani, 1991). Such environments are typified by high air and soil temperatures and radiation loads, and large saturation deficits, resulting in potentially rapid evapotranspiration which is often dominated by the soil evaporation component due to the sparse vegetation cover (Allen, 1990; Massman, 1992; Wallace *et al.*, 1993). Annual rainfall is generally lower than potential losses by evapotranspiration (Rosenberg, 1984), causing water stress; even in areas where mean annual rainfall exceeds potential evapotranspiration, water stress may be induced by local deviations from the regional average (Sivakumar *et al.*, 1984). The availability of water delineates the growing seasons (Zahner, 1968) and provides the greatest constraint to plant growth (Gindel, 1973; Lugo *et al.*, 1978; Monteith and Virmani, 1991). Additional constraints such as nutrient availability (Scholes *et al.*, 1994), high or low temperatures (Warrington and Kanemasu, 1983; Ong and Monteith, 1984; Jones and Kiniry, 1986) and susceptibility to erosion and waterlogging (FAO, 1994) may also limit crop growth. Classifications based on these criteria result in approximately one third of the global land area being defined as semi-arid.

The natural vegetation in semi-arid environments is generally dominated by grasslands or scrub forest. Both biomes may occur under similar climatic conditions, with their predominance being determined by factors such as rainfall distribution and

the occurrence of fire and high winds. When limited rainfall is distributed widely throughout the year, theoretical considerations and practical studies both show that scrubby woody perennial species are best adapted to the prevailing soil and climatic conditions (Ben Salem, 1980; Ben Salem and Palmberg, 1985). Perennial species frequently have a high capacity for self-protection conferred by a range of morphological, biochemical and physiological mechanisms (Steele *et al.*, 1985; Zhang *et al.*, 1988; Gates and Brown, 1988; Peltier *et al.*, 1990). These provide the necessary resilience to survive periods of adverse climatic conditions at the expense of reductions in, or complete cessation of, growth and development; when favourable conditions return, the full productive potential of such species is rapidly restored. As a result, perennial plants frequently provide environmental protection by providing continuous ground cover and stabilising the soil with their deep and extensive root systems (Lange *et al.*, 1976; Smith, 1995). The presence of perennial species also affords protection to other plants (and animals) growing in their shelter as a result of biological and micro-environmental improvements (Ben Salem and Palmberg, 1985). In contrast, naturally occurring annual species, such as those found in semi-arid grassland vegetation, lack such resilience to the effects of drought and adopt a drought-avoidance strategy by surviving dry periods as seeds which germinate rapidly following the onset of the rains. Such species must complete their life cycle during the short period when water is available, but since rainfall may vary greatly from year to year such a strategy may result in catastrophic failure. It is ironic therefore that most modern agricultural development in semi-arid zones has relied on annual tropical or temperate crop species which are poorly adapted to the prevailing climatic conditions (Nabhan and Felger, 1985), particularly the short and unreliable rainy seasons. Ben Salem and Palmberg (1985) consider the cultivation of inappropriate annual crops as one of the most common and unrecognised abuses of semi-arid ecosystems since their cultivation disregards the prevailing constraints to plant productivity in semi-arid environments. In addition, agricultural systems based on monocultures of annual crop plants leave the soil unprotected for extended periods and, when used unwisely, may deplete and impoverish the surface horizons which their shallow root systems colonise.

1.1.2 The developmental context

Current estimates suggest that the World's human population will increase from c. 5.7 billion to c. 9.4 billion during the next 50 years (Fischer and Heilig, 1996), and this increase will occur predominantly in developing countries. It has been predicted that this increase in human population and anticipated changes in diet will necessitate a six-fold increase in agricultural production relative to that currently harvested, and that this increase must be provided mainly through improvements in farming practices rather than expansion of the land area under cultivation (Fischer and Heilig, 1996). This is because little of the global land area that is potentially suitable for agriculture is not already in production; land currently occupied by forests and wetlands was discounted from this analysis due to their global environmental importance.

The socio-economic structure of the developing world, particularly in Africa, is not expected to change from the current smallholder system during the next 50 years (Sanchez, 1996). The potential of such a structure to support the entire food requirements of the local population is extremely limited, particularly given the low soil fertility and the poor adaptation of the major food crops to the prevailing climatic conditions; indeed, *per capita* food production in Africa has declined steadily since the 1970s (Hinman and Hinman, 1992). It is therefore essential that agricultural systems are developed which focus on high-value products that enable farmers to buy food, particularly cereals, from the existing highly productive grain belts of the world. Although agroforestry and horticulture may both offer a suitable technological framework, there is a need to select suitable products and integrate new agricultural systems with more traditional approaches so that the current requirements of the population are met throughout the establishment or 'payback' period. It is the impact of the technology on crop yields in the short term and the consequent ability of farmers to provide for their families that is often the key factor in determining whether new technologies are adopted.

The pressure of expanding populations on the agro-ecological base of the semi-arid tropics (SAT) is probably greater than in any other ecological zone (Wallace and Batchelor (1996). Favourable climatic conditions in the short term, coupled with the

Plate 1.2 View from the CIRUS experimental site showing extensive clearance and recontouring of land for agriculture which occurred on the opposite side of the Maruba River between March 1995 (Plate 1.1) and March 1997.

imposition of restrictions on traditionally nomadic societies, have led to the rapid expansion of dryland farming and cattle-rearing to an extent that cannot be supported in drier years (Goudie, 1988). The result has been rapid clearance of natural vegetation for cultivation, pasture and fuelwood. This is illustrated by comparing Plates 1.1 and 1.2 which show the rapid and extensive clearance of hillslopes for agriculture that continues to occur in the Machakos region, where this study was conducted, and in many other regions of the developing world. The collection of fuelwood in particular, which constitutes 80 to 90 % of the energy consumption in rural Africa (Foley, 1987), has caused a dramatic decline in live tree biomass in semi-arid areas where the population often exceeds the estimated carrying capacity for fuelwood of 40 persons km^{-2} (Swallow, 1995). This clearance of the natural vegetation results in subsequent degradation of the soil and drying of the local climate which are insidious processes that may lead to desertification. As a consequence, 1.8 billion people now require 25 % more water to reach self-sufficiency which, when combined with projected population growth, translates to over half the World's population becoming dependent on food and fuel imports within the next 30 years due to scarcity of water (Falkenmark, 1996). However, there is considerable scope to convert more of the blue water of semi-arid environments (runoff, standing water, evaporation, drainage etc.) to green water (virtual water held within agricultural production) through improved water management technologies, thereby reducing the impact of low rainfall on food and fuel production (Wallace and Batchelor, 1996). Such technologies reduce runoff by increasing infiltration and surface storage (e.g. terracing and bunding), reducing evaporation through shading, decreasing drainage and improving the water use ratio of crops by breeding and selection. The role of agroforestry in improving the management of available water supplies is reviewed below.

1.1.3 Potential benefits of agroforestry in semi-arid environments

Agroforestry is a collective term used to describe land-use systems in which woody perennials (trees, shrubs etc.) are grown in association with herbaceous species (crops, pasture) and/or livestock in a spatial arrangement, a rotation, or a combination of both (ICRAF, 1996). This definition is necessarily broad to encompass the huge diversity

of systems in which woody perennial species are incorporated as inseparable components of land use systems and represent essential elements of the rural economy. The motives for adopting agroforestry are wide-ranging but can be distilled into two main categories which are not mutually exclusive, i.e. environmental amelioration and improvements in the productivity of the land. Environmental amelioration includes the planting of shelter belt trees to reduce wind erosion and crop desiccation (e.g. van den Beldt, 1990; Smith, 1995; Brenner *et al.*, 1995) or to enhance the fertility and physical properties of the soil (e.g. van Noordwijk *et al.*, 1993; Marshall, 1995), and the use of contour-planted hedgerows on hillslopes to promote soil conservation (e.g. Young, 1989; Kiepe, 1995). Improvements in productivity generally result from the increased capture and conversion of resources resulting from continued vegetative growth throughout the dry season, thereby ensuring that the available resources are captured as effectively as possible.

Whenever plants are grown in close proximity, they interact spatially and temporally in their capture of the available resources, resulting in competition under resource-limiting conditions (Grime, 1974). This competition is generally more severe between similar species than between species with differing niches or growth habits (Vandermeer, 1989). This effect, known as Gause's hypothesis, is the principle underlying the success of mixed cropping in which competition is minimised by growing species with differing resource requirements on the same area of land. Ong (1995) coined the phrase "complementarity" to describe this positive association of species that results in increased system productivity. Complementarity may result either from increased resource capture or improved resource use efficiency (Stigter and Baldy, 1995), and may be either temporal or spatial. Temporal complementarity occurs when one species cannot fully exploit the available resources due to restrictions imposed by its growth habit (e.g. short duration species); mixtures of such species with other species with a compatible growth habit (e.g. slow growth and long duration) exploit the available resources more fully over time. Spatial complementarity occurs when the components of mixed communities occupy different niches, for example, when a shallow rooted species is combined with a deep-rooted species, allowing a greater proportion of the available resources within the system to be exploited.

In the annual cropping systems of semi-arid environments, resource capture and biomass production are confined to the growing period of the crops involved and the land lies bare for much of the year, particularly in areas of unimodal rainfall. However, residual water frequently remains in the soil profile after harvest and off-season rainfall may go unused. Work at ICRISAT Centre, India showed that substantial quantities of available water were left in the 45-90 cm horizons when short-duration sole sorghum was harvested, and that available water remained even after the longer duration sole pigeonpea was harvested three months later (Ong *et al.*, 1992). At Hyderabad, 20 % or 152 mm of the annual rainfall is received outside the normal cropping season. Agroforestry therefore offers considerable potential to increase productivity by exploiting off-season rainfall, residual water supplies in the surface horizons and, due to the more extensive root system of the trees, deep reserves of water beneath the rooting depth of annual crops. Additional benefits may be obtained by exploiting the potential of agroforestry as a water management tool for reducing the proportion of the annual rainfall that is lost to runoff, deep percolation and soil evaporation. The scope for such water management practices is considerable. For example, sorghum/pigeonpea intercrops grown on the alfisols of the Deccan plateau in India use only 41 % of the annual rainfall, while the remainder is lost as runoff (26 %) or deep drainage (33 %; Ong *et al.*, 1992). Similarly, Cooper *et al.* (1983) and Wallace (1991) reported that soil evaporation might account for 30-60 % of rainfall in semi-arid areas of the Middle East and West Africa. The physical barriers offered by the trunks and roots of trees may reduce the proportion of water lost to runoff, particularly on hillslopes, while their relatively high root density and deep rooting habit may restrict water losses by deep drainage. Shading by the tree canopy would potentially decrease soil evaporation, particularly during the early part of the season when the crop canopy is sparse and rain is received as frequent, low intensity events. Under these circumstances, evaporation is primarily energy-limited and so any reduction in the quantity of radiation reaching the soil is likely to reduce evaporation. Decreased windspeeds at ground level resulting from the sheltering effect of the trees would also be expected to reduce evaporation. In addition, soil water availability might be increased by improvements in water-holding capacity and infiltration as a consequence of increases in soil organic matter, resulting from decomposition of leaf litter or animal manure, and the maintenance of soil structure as

a result of the greater protection afforded by the denser ground cover. However, a possible disadvantage is that interception losses resulting from the evaporation of rainfall intercepted by the tree canopy, range from 10-30 % in agroforestry systems (Ong and Black, 1996).

The hypothesis that agroforestry may improve productivity by capturing a greater proportion of the annual rainfall has gained support in recent years. Ong *et al.* (1992) reported that hedgerow plantings of sole leucaena extracted more of the available soil moisture than sole crops or intercrops of sorghum and pigeonpea. Widely spaced alley crops (4.4 m between hedges) extracted even more water than sole leucaena, indicating that the agroforestry systems were most effective in utilising available moisture. Similarly, measurements of transpiration using the heat balance method showed that the annual transpiration of perennial pigeonpea grown in an agroforestry system with groundnut was 887 mm or 84 % of the annual rainfall, double the water use of the most productive sole crop system (Ong and Black, 1994). Almost half (47 %) of the total transpiration occurred between January-June, when only 211 mm of rain was received, indicating that 205 mm was extracted from soil reserves. In contrast, an excess of 420 mm received during the rainy season between July-November was lost as runoff and deep drainage. Sole pigeonpea was much less effective in preventing runoff (<=30 % of rainfall during high intensity storms) than either sole groundnut or the pigeonpea/groundnut intercrop (<=5 %). These results clearly emphasise the potential of agroforestry for increasing rainfall utilisation and productivity in the semi-arid regions of the tropics.

In addition to the increase in productivity resulting from greater capture of water by agroforestry systems, the presence of trees may modify the crop microenvironment in ways that may improve the yields of understorey crops. For example, Huxley *et al.* (1994) observed that the growth and yield of maize were increased by up to 80 % on the sheltered down-wind side of a tree line compared to unsheltered maize. Likewise, Huxley *et al.* (1989) found that the presence of shade during the afternoon provided considerable benefits for maize yields in a *Cassia*/maize agroforestry system during seasons of poor rainfall. These studies are by no means the only ones reporting benefits of shelter for crop yields (cf. Nicholas, 1988; Brenner *et al.*, 1995; Smith,

1995), although the exact nature of the microclimatic modifications remains unclear. Potential modifications to the crop microenvironment and consequent crop responses are reviewed in Section 1.2.

Agroforestry not only has the potential to increase overall productivity but also diversifies the product base, thereby providing a degree of risk limitation. For example, in the arid regions of India where groundwater is the predominant source of water, trees have been cultivated with annual crops for centuries as a contingency against crop failure in drought years (Sharma, 1992; Harsh *et al.*, 1993). In this case, the trees are used as a source of fodder and fuel, but other potential products include building materials, fibre, fruits, nuts, essential oils, gums, resins, tannins and pharmaceuticals (Ben Salem and Palmberg, 1985). In addition, a wider product range can result in a spread of harvests throughout the year, thereby providing a year-round source of income and a degree of economic stability (Thapa *et al.*, 1995).

1.1.4 Potential disadvantages of agroforestry in semi-arid environments

Thapa (1994) suggested that the potentially adverse effects of agroforestry were:

- allelopathy
- increased extraction of nutrients and water, causing more rapid depletion of below-ground resources
- harbouring of pests and diseases by the trees and associated micro-environmental changes which encourage the growth of weeds
- limitation of understorey crop growth by shading
- increased crop management problems, particularly in mechanised and high input systems

Predicting the occurrence, form and extent of any disadvantages associated with agroforestry is complex. For example, *Grevillea robusta* windbreaks in orange orchards in Cape Province, South Africa were found to harbour citrus thrips (Grout and Richards, 1990). In contrast, *Pinus radiata* and *Casuarina cunninghamiana* trees within the same trial were found to be free of citrus thrips but instead harboured large

populations of the citrus mites that prey on thrips. The relative advantage or disadvantage associated with agroforestry systems might therefore be construed as being largely species-dependent, although there is the potential for important interactions with other factors such as environment and management. In addition, farmers are often aware of the negative effects of agroforestry, but make calculated decisions in which the anticipated overall benefits of the system (often the economic return from the tree component) are weighed against the disadvantages (Hoekstra *et al.*, 1991). For example, the reduced productivity of understorey beans associated with avocado trees in Burundi is offset by the sale of avocado fruit and their nutritional value during periods of the year when there are food shortages (Guinard *et al.*, 1992).

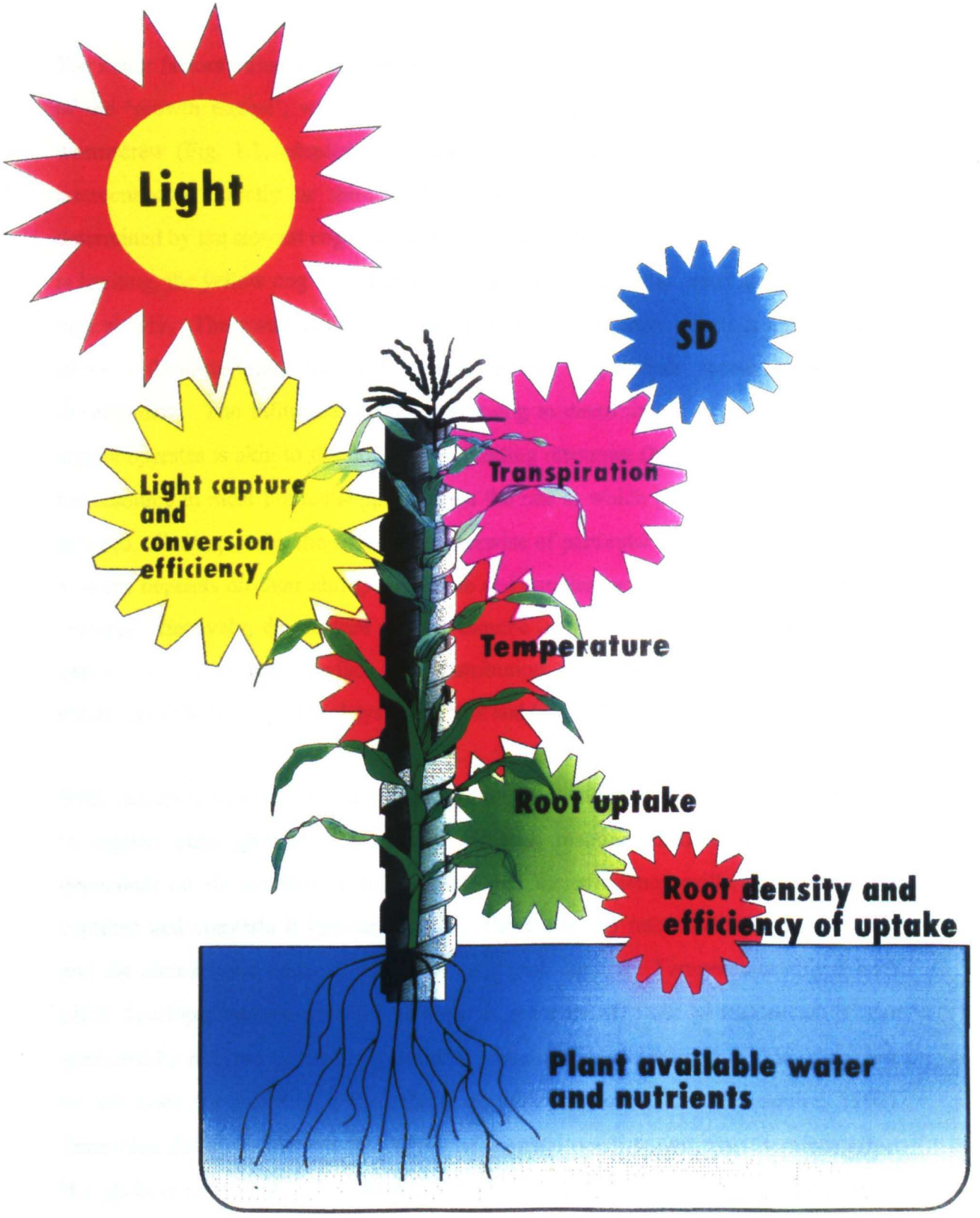
1.2 COMPONENT INTERACTIONS AND PLANT PHYSIOLOGICAL RESPONSES IN DRYLAND AGROFORESTRY

Interactions between the components of agroforestry systems are multi-faceted (Alpizar *et al.*, 1986) and relate particularly to climatic (solar radiation, temperature, rainfall, wind and relative humidity), soil conditions (organic matter, nutrients, water), plant health (pests and diseases) and bio-ecology (symbiosis, alotropia, allelopathy, parasitism). Such wide scope for interaction gives rise to tremendous complexity in the design and management of effective agroforestry systems. In addition, these complexities are compounded by the changing pattern of resource capture as the system matures. For example, the interactions that occur between the components of agroforestry systems when the trees are young saplings may be expected to be very different from those associated with mature trees. Thus both the degree and nature of complementarity (spatial or temporal) between the components of agroforestry systems will vary with time.

During the establishment phase of agroforestry systems, the young saplings are relatively short and the canopy has a limited leaf area. It is therefore likely that the tree component will be shaded by the crop component during establishment and will also experience considerable below-ground competition. This situation will persist to a greater or lesser degree until the canopy and root system of the trees are sufficiently

Figure 1.1 The Growth Engine: A pictorial representation of the major factors influencing crop growth in dryland areas (adapted from Bradley and Crout, 1994)

The Growth Engine



established to compete effectively with associated crops. Consequently, although the tree is considered to be the dominant system component, the crop is likely to have an impact on tree growth during the early establishment phase.

The major factors influencing crops growing in dryland areas are illustrated by the cogs of the 'growth engine', while crop growth and development are represented by the wormscrew (Fig. 1.1, adapted from Bradley and Crout, 1994). Since the cogs are interconnected directly or through the wormscrew, the engine operates at a rate determined by the slowest cog. Thus, for example, if the light level is optimal but water is limiting, the yellow cog will attempt to turn quickly while the green and orange cogs turn slowly. The result is torque manifest in the wormscrew which is equivalent to stress within the plant that inhibits growth and may either accelerate or retard development. The influence of the slowest cog in determining the rate at which the engine operates is akin to the principle of limiting resources (Monteith, 1981) in which the resource in most limited supply defines the rate at which growth and development proceed. Consequently, the success or otherwise of particular crop species or cropping systems depends on their ability to capture and use the most limiting essential growth resource effectively; the capture of this resource (i.e. light, water or nutrients) in turn depends on the number, surface area, distribution and effectiveness of the individual elements of the canopy or root system (Black and Ong, 1998).

Solar radiation, soil nutrients and soil moisture are the three primary resources required to support plant growth. The quantity of each resource utilised by the plant is dependent on its availability to the plant and the efficiency with which the plant captures and converts it into dry matter. There are two rate modifiers: temperature and the atmospheric demand for water (saturation deficit). Temperature affects both plant development and growth, as well as a range of other processes which are mediated by enzyme controlled reactions, including photosynthesis, and is often used as the basis for examining the effects of other influential factors (Squire, 1990). Saturation deficit influences the degree of stomatal opening and may therefore affect the photosynthetic rate (Coombes and Hall, 1982). The present study focused on temperature, solar radiation and water, each of which is explored in greater detail below.

1.2.1 Temperature

As meristem temperature is of fundamental importance in determining the metabolic activity of plant tissues (Ehleringer, 1989), shading by the overstorey component of agroforestry systems may alter the temperature environment experienced by understorey components in ways that may be either beneficial or detrimental for phenology and productivity. Growth and development increase with temperature up to an optimum, beyond which the rate declines. In areas of high radiation and ambient temperature, tissue temperature may regularly exceed optimal levels in unshaded sole crops, particularly during drought periods, causing growth and development to be greatly delayed. Partial shade may therefore have an ameliorating influence by bringing tissue temperatures within the optimum range, thereby reducing exposure to thermal stress. For example, Jonsson (1995) observed that flowering and maturity of pearl millet grown in Sapone, Burkina Faso were delayed by 10-12 days when soil temperature exceeded 40 °C for several hours during the day, while McIntyre *et al.* (1993) suggested that high soil temperatures in northern Nigeria reduced both leaf growth and the conversion coefficient for pearl millet. However, millet seedlings growing in the shade of nere (*Parkia biglobosa*) and karite (*Butyrospermum parkii*) trees rarely experienced supra-optimal temperatures and should therefore experience some physiological advantage over unshaded sole crops (Jonsson, 1995). In order to quantify and predict the extent of any thermal advantage, the concept of thermal time has been developed and is reviewed below.

The rate at which plant growth and development proceeds generally increases almost linearly between a base temperature (T_b) and an optimum (T_o) where it reaches its limit, before declining again between T_o and a maximum (T_m) where the process ceases; T_b, T_o and T_m are termed the cardinal temperatures and may vary widely between species or genotypes. The quantity of chronological time required to complete specific developmental processes therefore declines as temperature increases between T_b and T_o, but increases between T_o and T_m. Many studies have used these cardinal temperatures to ascertain the impact of the thermal environment on the duration of crop growth and development periods. The horticulture industry in particular has led much of the development of this concept due to the need for accurate predictions of harvest dates

during the relatively short period when vegetable crops are of the high quality demanded by food retailers and consumers (Cross and Zuber, 1972). In addition, breeders and farmers both required detailed information on the duration of growing periods so that the life cycle of crops could be matched to the availability of resources within specific growing environments in order to maximise productivity (Corke and Kannenberg, 1989). From these requirements and the associated early work arose the concept of thermal time, which is essentially the product of chronological time and the temperature increment above T_b experienced by the plant and is conventionally expressed in units of degree days (°Cd; Hawkins and Cooper, 1981; Garcia-Huidobro *et al.*, 1982a; Ong and Squire, 1984; Ong and Monteith, 1985; Mohamed *et al.*, 1988; Corlett *et al.*, 1992a). However, thermal time calculations should also take account of the slower rates that occur when temperature exceeds T_o by including the range between T_o and T_m within the calculation.

The thermal environment influences the ability of crops to capture resources by determining the size and longevity of both the canopy and the root system which represent the two resource capture surfaces. The overall area of these resource capture surfaces depends on both the number of individual elements or sub-units (e.g. individual leaves or root branches) and the mean area or length of each element. More rapid thermal time accumulation increases the rate of initiation of primordia for individual elements and their subsequent rate of expansion. Thus reduced rates of thermal time accumulation resulting from overstorey shading in agroforestry systems might be seriously disadvantageous for resource capture by the understorey component. However, during other developmental stages, slower rates of thermal time accumulation might confer a considerable advantage. For example, in crops such as maize, slower rates of thermal time accumulation could increase the potential number of grains per ear by lengthening the duration of the grain set period (Rosenthal *et al.*, 1989). In addition, shading may reduce the period of time that the understorey plants are exposed to stress temperatures, which can greatly reduce the number of reproductive primordia (Squire, 1990).

1.2.2 Solar radiation

Numerous field experiments using various crops have shown that a linear relationship frequently exists between total dry matter production and intercepted radiation during the growing season, provided environmental and cultural constraints are minimal (cf. Monteith, 1977; Jordan, 1983; Squire *et al.*, 1987; Monteith *et al.*, 1991). This relationship therefore takes the form:

$$W = S f e \qquad \text{Equation 1.1}$$

where W represents total plant dry weight, S denotes total incident solar radiation, f is the fraction of the incident solar radiation that is captured by the canopy and e is the radiation conversion coefficient. Agroforestry in semi-arid environments has the potential to influence all three of the factors which determine W; each is considered below, while more thorough reviews are provided by Ong *et al.* (1996) and for intercropping by Keating and Carberry (1993).

Under semi-arid conditions, plant growth is unlikely to be limited by S since radiation receipts are generally high, frequently exceeding 24 MJ m^{-2} d^{-1} (Squire, 1990). However, a reduction in solar radiation incident on understorey canopies is probably the most conspicuous impact that establishing an overstorey agroforestry system may have on resource capture. The intensity of shading depends on factors that govern f for the overstorey canopy as well as the slope and aspect of the site. The influence of reductions in S on the understorey component depends largely on its ability to maintain high photosynthetic rates under reduced radiation levels. In general, the photosynthetic rate of C3 plants is less affected by shade than in C4 species because the former becomes light saturated at lower radiation levels, with the result that reductions in S may have little effect on the net rate of photosynthesis (Salisbury and Ross, 1992). In addition, the reduced quantity of radiation received by the understorey crop tends to reduce transpiration and thereby increases water use efficiency. The potential benefits of shade are therefore likely to be highly dependent on the intensity of shading and the photosynthetic pathway of the crop involved.

The fraction of incident radiation intercepted by vegetation canopies depends on the area, orientation, distribution and longevity of the leaves as well as their transmittance and reflectance (Squire, 1990). Consequently, the seasonal timecourse of *f* varies greatly depending on canopy architecture and the phenology of the vegetation involved; *f* increases more rapidly in cereals such as sorghum than in legumes such as groundnut, reflecting their differing rates of leaf initiation and expansion (Black and Ong, 1998). Environmental variables that influence canopy size also have an important role in defining *f*, and these influences can be broken down into those which affect the rate of leaf emergence and senescence (e.g. temperature) and those which affect leaf expansion (e.g. water and nutrient availability; Squire, 1990). Thus any interactions between the components of an agroforestry system which alter those environmental variables which influence the size of either component canopy compared to their respective sole stands will affect *f*.

Mean *f* values calculated over the duration of the crop are generally lower in short-duration cereals (c. 0.5) and legumes (c. 0.15) than in perennial species (c. 0.9), largely because of the differing duration of ground-cover (Squire, 1990). Consequently, the provision of a perennial tree component in agroforestry systems should raise *f* for the system as a whole despite potentially negative interactions that may affect values of *f* for either the tree or the crop component. Indeed, Ong *et al.* (1996) suggested that the primary goal of agroforestry is to increase *f* values and hence overall dry matter production; this contrasts with intercropping where improvements in productivity are often attributable to increased conversion coefficients. For example, the *Leucaena leucocephala*/millet alley cropping system described by Monteith *et al.* (1991) and Corlett *et al.* (1992a, b) intercepted a substantially greater fraction of the incident radiation during the 1986 rainy season than either of the monocrops. This was primarily because the presence of leucaena increased *f* during the early stages of the growing season, while the millet provided a more complete ground cover across the alleys during the later stages of the season.

The conversion coefficient *(e)*, defined here as the quantity of biomass produced per unit of intercepted radiation (g MJ^{-1}), provides a measure of the "efficiency" with which the captured radiation is used to produce new plant material (Black and Ong, 1998); the

alternative term, radiation use efficiency (RUE), is also commonly used. *e* essentially represents the rates of photosynthesis and respiration and, in the absence of stress, is often conservative, typically ranging between 1.5-1.7 g MJ^{-1} for tropical C3 species (Kiniry *et al.*, 1989; Monteith, 1990) and up to 2.5 g MJ^{-1} for tropical C4 cereals under favourable conditions (Squire, 1990). In semi-arid environments, however, drought is likely to induce substantial reductions in *e* by decreasing photosynthetic rate as a result of low soil moisture availability and high saturation deficits. Thus any interactions between the tree and crop components of agroforestry systems which influence either soil moisture content or saturation deficit are likely to affect the values of *e* for either or both of the components. However, the response of *e* is difficult to predict since the interactions between trees and crops are tremendously complex in terms of the environmental modifications which may be induced and because the environmental factors that govern *e* are usually closely coupled.

1.2.3 Water

Section 1.1.3 described agroforestry in terms of its potentially greater utilisation of soil moisture through capturing off-season rainfall, exploiting reserves of soil water below the crop rooting zone and acting as a water management tool to reduce the proportion of the annual rainfall that is lost to runoff, deep percolation and soil evaporation. This section examines the impact that the overstorey component may have on the capture and use of soil moisture by understorey crops.

The quantity of dry matter produced (W) depends on the quantity of water captured and the "efficiency" with which this is used to produce dry matter. An equation describing this relationship would therefore take the form:

$$W = e_w E_t \qquad \text{Equation 1.2}$$

where E_t represents cumulative transpiration and e_w denotes the water use ratio, a term equivalent to the conversion coefficient for radiation (*e*). W is often linearly related to the quantity of water transpired, indicating that like *e*, e_w is conservative (de Wit, 1958; Azam-Ali, 1983; Connor *et al.*, 1985; Cooper *et al.*, 1987). This relationship depends

on the close linkage between CO_2 and water vapour fluxes due to the role of stomata in regulating the exchange of both gases. However, saturation deficit may exert a strong modifying influence on e_w.

Water is the dominant factor limiting plant production in dry environments (Soegaard and Boegh, 1995). Under conditions of water deficit, conservation measures adopted by plants to conserve water status are likely also to limit CO_2 assimilation, and thereby reduce the production of photosynthates (Salisbury and Ross, 1985). In addition, increases in leaf temperature resulting from water stress may increase respiration, further retarding growth (Rosenberg *et al.*, 1983). Shading provided by the tree canopy in agroforestry systems could alter the microenvironment experienced by understorey crops in a manner which favours greater water uptake or increases water use efficiency, thereby reducing the frequency and severity of water stress and improving productivity. There are several ways in which tree shade can potentially modify the microenvironment to the benefit of understorey crop growth and these are discussed below.

Direct evaporation of soil moisture from agricultural land in the semi-arid tropics is frequently responsible for rapid water loss as a result of incomplete canopy cover exposing extensive areas of bare ground for much of the year (cf. Section 1.1.3). Direct soil evaporation under these conditions is dominated by radiation, wind speed and relative humidity at the soil surface (Wallace, 1996). Consequently, the presence of the tree canopy in agroforestry systems might reduce soil evaporation, by decreasing radiation or windspeed, or by increasing humidity, and thereby increase the quantity of soil moisture potentially available for uptake by the tree and crop components of the system. In addition, leaf litter from the tree canopy may act as a surface mulch which could further reduce soil evaporation.

Monteith (1988) demonstrated that e_w is inversely related to the atmospheric saturation deficit. The humidifying effect of transpiration from both the tree and crop canopies, coupled with reduced understorey windspeeds, might therefore be expected to reduce the within-canopy saturation deficit, and thereby increase e_w (Wallace, 1996a). Shading of the understorey crop may also reduce transpiration without

adversely affecting photosynthesis. As discussed in Section 1.2.2, C3 plants may become light saturated at relatively low radiation levels, with the result that their photosynthetic rate may be unaffected by partial shading. As shading may also reduce transpirational demand, the net effect may therefore be to increase e_w (Ong *et al.*, 1996).

The degree to which agroforestry provides more favourable conditions for crop growth is dependent on the degree of shading afforded by the tree canopy, the prevailing environmental conditions and the physiological characteristics of the understory crop (Wallace, 1996a). However, as the principles governing the interactions between tree and crop components are complex and poorly understood (Brenner, 1996), it remains difficult to predict the circumstances under which the favourable interactions described above are likely to occur.

1.3 SYSTEMS MODELLING

Ong (1995) stated that the two fundamental design and management objectives in processed-based agroforestry research are:

- to maximise beneficial tree-crop interactions and resource use

- to develop a predictive capability for extrapolating the results to new environments over extended periods.

While current knowledge concerning the environmental physiology of the components of agroforestry systems is relatively advanced, combining these elements to describe the functioning of the system as a whole and to make predictions concerning its likely behaviour is extremely complex (Lomnicki, 1988). Consequently, research directed towards these fundamental objectives requires highly focused field experiments to be combined with mathematical modelling to better understand the complex interactions that occur in agroforestry systems. However, the structure of models developed in agroforestry research should differ according to which of the above objectives it is designed to fulfil (Penning de Vries and Spitters,

1991). Models used to promote a greater understanding of the principles underpinning interactions between the components of an agroforestry system should emphasise the integration of current process-level knowledge. However, applied models intended for extrapolation to new conditions should emphasise simplicity by ensuring a mechanistic structure based on a small number of essential parameters. It is better for applied model output (and the model) to be relatively simple and therefore understandable, even if not totally accurate in its predictions, than to try and account for all potentially influential factors and be lost in the resultant confusion (Monteith, 1996). This is particularly pertinent to complex, physiologically-based models which may not provide more accurate results than simpler models because the information required to parameterise them is unavailable. In addition, most models represent a balance between mechanistic and empirical approaches and are therefore based on a combination of proven physical or physiological factors and algorithms chosen arbitrarily to fit measurements made under field or laboratory conditions (Monteith, 1996). It is important that the empirical aspects of models are kept to a minimum to maintain their general applicability, particularly during model calibration when the temptation is to arbitrarily alter model parameters and structure in order to match simulated output with observed experimental values. This process however adds little to the general understanding of the system nor helps to provide a reliable tool to extrapolate results to other environments.

1.4 Species choice

The main requirements for species choice in this study were the rapid establishment of an overstorey tree canopy and the ability to examine the responses of understorey crops possessing the C4 and C3 photosynthetic pathways; as discussed earlier, the yield of C3 crops may be less affected than C4 species by the understorey environment. In addition, the species chosen had to be locally available and adapted to the prevailing environmental conditions. Consequently, *Grevillea robusta* was selected as the tree component and maize and cowpea respectively as the C4 and C3 understorey crops.

1.4.1 *Grevillea robusta*

Grevillea robusta A. Cunn. ex R. Br. is known as Silky or Silk oak and sometimes as Silver oak, although the latter common name is also used to describe a member of the Compositae, *Brachylaena huillensis*. In addition, *Grevillea robusta* is commonly called grevillea in Kenya and much of East Africa and consequently it is this common name that has been adopted throughout this thesis. Grevillea is a member of the dicotyledonous angiosperm family, the Proteaceae (Boland *et al.*, 1984). Native to Australia, grevillea occurs naturally along a 160 km wide coastal strip stretching from North New South Wales to Southern Queensland and hence encompasses a wide ecological range (Harwood and Getahun, 1990). Within this natural habitat, precipitation ranges from 720 to 1710 mm and altitude from near sea level to 1120 m (Harwood, 1992b). Optimum climatic conditions comprise 1000-2000 mm of rainfall per annum (the incidence of fungal attack is high above 2000 mm) and mean temperatures of 15-18 °C, although grevillea will grow under low rainfall conditions (400-600 mm) and can survive frost (Harwood and Getahun, 1990). Grevillea responds favourably to soils which are reasonably fertile and well drained and tolerates a wide pH range, although strongly acidic soils may pose problems (Harwood and Getahun, 1990).

Grevillea robusta is the largest species in the genus, reaching a maximum height of c. 40 m and diameter at breast height (dbh) of c. 1 m (Harwood and Getahun, 1990). Under optimal conditions, annual height increments of 2 m may be expected during the first 5-10 years, while annual increments of 1 m are obtained under drier conditions (600-800 mm rainfall). Grevillea is facultatively deciduous, continuously maintaining a full canopy, with leaves surviving for over 12 months except during prolonged drought (Harwood, 1992b). Despite this, grevillea is not recommended for East African gardens because of its copious leaf fall and brittle branches. Its leaves are large and pinnately compound, possessing numerous leaflets with well defined lobes, and exhibit xeromorphic features, being leathery, hardy and evergreen (Thimma Raju, 1992), and so are well suited to dry conditions. Pollination of the large yellow flowers is primarily by birds and the seeds have wings for wind dispersal. Grevillea is generally free of pests within its natural range (Harwood, 1992b) but elsewhere is susceptible to some diseases, notably *Asterolecanium pustulans* which has virtually eliminated grevillea from parts of

the Caribbean (Harwood and Getahun, 1990). In addition, termite attack is a major problem on low rainfall sites in Africa (Harwood and Getahun, 1990).

Laycock and Wood (1963), Jonsson *et al.* (1988) and Mwihomeke (1993) all suggested that *Grevillea robusta* has a high potential for spatial complementarity with annual or perennial crops because it produces few superficial lateral roots with most roots being orientated in a predominantly vertical plane (cf. Skene *et al.*, 1996). Selection programmes for grevillea, however, have been led by breeders wishing to exploit its economic potential for timber and pole production, and have therefore not focused on encouraging this deep rooting habit or on other compatibility traits useful in agroforestry such as a sparse and narrow crown (Harwood and Owino, 1992). Consequently, Owino (1996) found wide variation in the root distribution of grevillea in a study of 154 tree 'families', with a significant proportion of individuals exhibiting 'non-compatible rooting habits'.

Grevillea robusta, like most members of the Proteaceae, has cluster roots (cf. Skene *et al.*, 1996). These dense clusters of rootlets allow full exploitation of localised areas of high nutrient availability, particularly of phosphorus. They are not produced specifically in response to nutrient-rich areas, but are controlled by the nutrient status of the plant and the distribution of its roots (Skene *et al.*, 1996). Lamont (1982) suggested that the uptake of P by cluster roots is 2-13 times greater than that by ordinary roots when expressed on a unit weight basis, suggesting that grevillea might increase the pool of phosphorus available to crops by mining deep-seated reserves and recycling them in litter fall.

Grevillea was first used as a shade and shelter-belt species in the tea plantations of Ceylon in the 1860s and later extended to the tea and coffee plantations of East Africa before 1900 (Harwood and Getahun, 1990). Its popularity in tea plantations stemmed from its open feathery crown which provided protection from direct radiation without casting intense shade and its deep root system, which was believed to bring up nutrients from deeper horizons, thereby making them accessible for tea growth following the decomposition of leaf litter. This litter also had the additional benefit of preventing 'surface wash' whilst decomposing on the ground (Anon, 1897). However, there are

conflicting views as to whether yield in tea is suppressed close to the trees (Visser, 1960; Othieno, 1983). Grevillea is still extremely popular and is currently grown in South and Central America, the Southwest Pacific, Malaysia, India, Madagascar and the African continent. Its popularity in Kenya may be illustrated both by a survey of tree nurseries conducted by Ongugo (1992), who found that demand exceeded supply, and also by the theft of newly planted grevillea saplings from multi-species trials in Machakos District (Williams, 1997); the thieves preferentially selected grevillea over all other species. Grevillea has been extremely successful as an agroforestry species planted along boundaries or scattered through fields in Eastern and Central Africa, Madagascar and Ethiopia (Harwood, 1989). However, monocultural plantations have been difficult to establish in Australia despite some success elsewhere due to auto-allelopathy, in which seedling growth is suppressed by water-soluble exudates secreted from the roots of adult trees (Harwood and Getahun, 1990). Grevillea is also used as an intermediary species in the afforestation of disturbed areas of tropical rain forest such as Karnataka, India where it is planted to prevent invasion by unwanted tree species in clear-felled areas and also to limit erosion on steep slopes in this high rainfall region (Kushalapa, 1988).

The success of grevillea in agroforestry stems from its reputation as a multi-purpose tree that is easy to manage and propagate from seeds, cuttings or stem grafts. It also offers potentially good yields of strong construction poles and high quality firewood whilst maintaining a low degree of competitiveness with crops (Harwood and Getahun, 1990). Indeed, in some cases, grevillea has been reported to enhance crop growth close to the trees (Harwood and Getahun, 1990; Evans, 1990; Spiers and Stewart, 1992; Akyeampong and Munyemana, 1993), although the compatibility of individual systems depends to a large degree on tree density (Akyeampong *et al.*, 1995); this in turn is highly site-specific depending on both biophysical and socio-economic constraints. Tyndall (1993) reported a mean density of 30 trees ha^{-1} for boundary-planted trees on small farms (1.8 ha) in the Kirinyaga area on the slopes of Mount Kenya, whereas Spiers and Stewart (1992) found that farmers in the relatively wet Embu and Meru Districts (900-1500 mm of rain) of Kenya planted grevillea in woodlots at densities of 1100-1600 trees ha^{-1} which were intercropped until the canopy closed. Ongugo (1992) reported that the optimum density for maximum system productivity when grevillea was

inter-planted with maize and beans in Rwanda was 400-600 trees ha^{-1} after 4-6 years and 250-300 trees ha^{-1} after 9-10 years. Pollarding grevillea increases growth rate and improves timber and pole quality, and hence the economic return (Spiers and Stewart, 1992), as well as reducing competition with associated crops.

Grevillea has some potential as a cash crop. The timber is comparable to beech and can be used for flooring and the manufacture of light furniture and plywood. The flowers have a high potential for honey production and the gum may be economically useful (Harwood and Getahun, 1990). It might also be used as a source of pulp for the production of cellulose-based materials such as viscose rayon fibre (Madan and Tandon, 1991). However, the main commercial uses for grevillea grown within agroforestry is as poles for construction, or as firewood in areas where firewood production has been commercialised, such as Kabale District, Uganda (Peden *et al.*, 1996).

The potential for using grevillea prunings as a surface mulch to control erosion and runoff is limited because its large leaf size is less capable of protecting the soil surface than smaller leaves such as those of *Cassia simea* (Omoro and Nair, 1993). In addition, Yobterik *et al.* (1994) conducted a pot trial using maize in which tree mulches were incorporated into the soil and found that maize yields were suppressed relative to the control by grevillea mulch. As was also suggested by Child and Smith (1960), the suppression of yield in maize was attributed to manganese toxicity resulting from its high concentration (5.8 %) in grevillea mulch (twig and leaf); this value was up to 13 times higher than for the other tree mulches examined, such as *Leucaena leucocephala*, *Gliricidia sepium* and *Cassia siamea.* However, these authors recognised that pot experiments can only reflect possible trends under field conditions and not necessarily the magnitude or dynamics of the response, especially since the mulch was finely ground and applied at high loadings under ideal moisture conditions. The C:N ratio of grevillea mulch is high (29.4 %) and its N concentration (1.79 %) is considerably lower than in leguminous species such as *Leucaena leucocephala* and *Gliricidia sepium* (4.20 and 4.25 % respectively); there is therefore a high potential for nitrogen immobilisation.

1.4.2 Maize

Maize (*Zea mays* L.) has the highest production potential of the three main cereal crops grown in the sub-humid to semi-arid tropics provided water and soil fertility are not limiting, but is the most drought-sensitive of the C4 crop species (Carberry *et al.*, 1989; Squire, 1990). Consequently maize is traditionally replaced with sorghum and then with millet in areas of decreasing rainfall (Carberry *et al.*, 1989). However, due to the favourable taste and ease of preparation of maize, coupled with the development of specific varieties adapted for growth under semi-arid conditions and the lack of success in breeding bird resistant grain sorghum, maize cultivation has progressively expanded into increasingly drier areas. Consequently, more countries cultivate maize world-wide than any other cereal with 58% of the area sown located in developing countries, although this area produces only one third of the global production which highlight the differences in yields obtained in developed as compared to developing countries. Global production of maize is the third greatest of all agricultural crops after wheat and rice, with an estimated yield in 1988 of 349 million tonnes from a cultivated area of 127 million hectares (FAO, 1994). In areas of the developing world where cultivation of wheat and rice is minimal, average per capita consumption of maize is approximately 100 kg yr^{-1}, equivalent to 40 % of the total calorie intake (Fischer and Palmer, 1984). Maize is the major cereal crop in Kenya and is grown at altitudes extending from sea-level to 2800 m, corresponding to mean annual temperatures ranging from 13 to 27 °C and rainfall of 250-1600 mm (Lenga and Keating, 1990). Reviews of the physiology and agronomy of maize are provided by Purseglove (1972), Fischer and Palmer (1984), Norman *et al.* (1984) and Lyamchai *et al.* (1996).

The initial response of maize to water stress is to exhibit leaf rolling prior to wilting, which reduces the heat loading on the leaves and shields the stomata from direct contact with solar radiation and the atmosphere (Fischer and Palmer, 1984). However, if drought persists, green leaf area is rapidly reduced as a consequence of reduced cell elongation and accelerated senescence of the lower leaves (Bolanos *et al.*, 1993). In addition, the occurrence of drought during the early stages of flowering irreversibly limits the number of grains set because delayed silking limits the number

of receptive silks present at the time of pollen release (Hall *et al.*, 1982). The occurrence of drought during the grain filling period (anthesis to silking) reduces assimilate partitioning to individual grains (Fischer and Palmer, 1984). Breeding programmes for drought-adapted maize varieties have therefore concentrated on selecting rapidly maturing cultivars capable of maintaining higher leaf water status under drought conditions in order to retain green leaf area and hence assimilate production, and to shorten the interval between anthesis and silking (Bolanos *et al.*, 1993).

Weed species pose greater problems for maize production than either pests or pathogens (Loomis and Conner, 1992); the parasitic angiosperm *Striga gesnerioides* in particular has a devastating effect on maize production in Kenya (Buresh, pers. comm.)

1.4.3 Cowpea

Cowpea (*Vigna unguiculata* (L.) Walp.) is an important staple crop in the subsistence farming communities of semi-arid Asia and Africa, as well as being an important fodder source (Steele *et al.*, 1985), a pot herb for the continuous production of 'spinach' which is particularly important in filling the 'hungry period' immediately preceding the main harvest (Purseglove, 1972), and in more advanced agricultural production as a forage or cover crop (Steele *et al.*, 1985). Although global production is not significant in terms of world trade, with an estimated annual production in 1981 of 2.3 million tonnes of dry grain from 8 million hectares of land (Rachie, 1985), cowpea is nevertheless extremely important at the local scale where it may provide more than half of the plant protein in human diets (Steele *et al.*, 1985). In the Machakos region of Kenya, cowpea represents the third most important crop species, ranked behind maize and beans. Exhaustive reviews of the physiology and agronomy of cowpea are given in Purseglove (1972), Summerfield *et al.* (1974), Wein and Summerfield (1984), Steele *et al.* (1985) and Summerfield *et al.* (1985).

Cowpea is particularly well adapted for growth in semi-arid environments largely due to its short duration growth habit, which can be as little as 65 days in varieties grown in

more arid environments (Hall and Patel, 1985). The variety grown in the Machakos area is an 80-day genotype bred locally by the Kenyan Agricultural Research Institute at the Katumani Research Station. Despite its short duration, yields can be relatively high, as demonstrated by the 1.6-3 t ha^{-1} obtained 85 days after planting by Summerfield *et al.* (1985) for cowpea grown under semi-arid rainfed and non-fertilised conditions. Cowpea limits stress by adopting drought-avoidance strategies such as decreasing its leaf area, changing leaflet orientation, and decreasing stomatal conductance (Summerfield *et al.*, 1974). As a consequence, the crop requires 'adequate water' for only 65 % of its life cycle (Summerfield *et al.*, 1985). The degree of drought tolerance is genetically determined, with particular differences occurring between determinate and indeterminate cultivars in response to the timing of stress (Summerfield *et al.*, 1974).

Pests and pathogens are the primary source of yield losses in cowpea in Africa and frequently cause complete crop failure (Steele *et al.*, 1985). Emechebe and Shoyinka (1985) listed over 20 major insect pests associated with cowpea in Africa, while Thottappilly and Russell (1985) identified 28 viruses. Emechebe and Shoyinka (1985) also noted the dramatic adverse effects that fungi, bacteria and nematodes may have on cowpea yields. Pests and pathogens may attack the cowpea crop at any stage of the cropping cycle, including seeds in storage.

1.5 Background to the project

In 1993, the UK Department for International Development (DFID, formerly the Overseas Development Administration) instigated the Agroforestry Modelling Programme (AMP) as part of its Renewable Natural Resources Research Strategy 1995-2005 to fulfil the remit of increasing the contribution of trees to the productivity of tree/crop systems. At an early stage of the programme, members of AMP identified the need to obtain a detailed fundamental understanding of resource capture and use within specific agroforestry systems in order to support the development and validation of process-based agroforestry models. Simultaneously, a planning workshop held in Nairobi in 1992 and attended by independent consultants with a wide range of expertise, identified the need for strategic research into resource capture and use in overstorey agroforestry systems. During this meeting, the University of Nottingham and the

Institute of Hydrology (IH) were identified as joint international collaborators in ICRAF's resource utilisation programme. The three institutes subsequently developed a co-ordinated programme to improve the understanding of tree/crop interactions in overstory agroforestry systems over a five-year period. This formed an integral part of ICRAF's Complementarity In Resource Use on Sloping Land (CIRUS) programme which had been established in 1991. DFID subsequently provided financial support to IH (grants R4853 and R6363), to carry out hydrological investigations in CIRUS, including belowground competition. Nottingham was initially funded by NERC and later by DFID (grant R5810), the Royal Society and the University of Nottingham Research Fund, to carry out intensive studies of water and light utilisation by the trees and crops in CIRUS and to apply this information to test the agroforestry model developed by AMP. The NERC award permitted these studies to be initiated in 1992 and 1993 (Howard, 1997), while DFID contract R5810 enabled them to be continued between 1994 and 1996; such long-term studies of tree/crop interactions in established agroforestry systems are rare. The integrated programme that was developed resulted in some activities being shared to optimise the use of available expertise, equipment and human resources. Consequently, while this thesis concentrates primarily on work carried out by the author, it occasionally draws on data gathered by collaborators; these are cited accordingly.

1.6 AIMS AND OBJECTIVES

The specific objectives of the work that forms the basis of this thesis were to:

(i) determine the transpiration, light interception and resource use efficiency of trees (*Grevillea robusta*) and crops grown in an established agroforestry system containing mature trees;

(ii) establish the impact of the trees on the growth of understorey crops with differing responses to shade (maize, cowpea);

(iii) test the integrated tree and crop growth model under continual development by AMP using the database compiled during the field campaign.

In the longer term, the research was intended to contribute to improving the productivity and sustainability of agricultural systems in semi-arid areas of the developing world and to increase the opportunities for resource-poor farmers working marginal land on hillslopes.

Table 2.1 Monthly, seasonal and annual rainfall (mm) at Machakos: historical means and recorded values for CIRUS between planting and project end (October 1991-July 1997).

	Average*	1991	1992	1993	1994	1995	1996
January	50	23	28	283	1	39	0
February	50	13	4	110	90	77	80
March	105	48	5	41	87	152	11
April	183	77	164	35	92	111	69
May	56	89	68	14	15	33	56
June	11	4	17	21	0	0	10
July	4	11	7	1	5	6	-
August	4	11	1	3	5	5	-
September	5	5	1	1	3	6	-
October	43	47	40	10	61	106	-
November	175	175	126	162	310	36	-
December	96	150	214	118	141	95	-
Long growing season (1 March - 31 July)	359	229	261	112	199	302	-
Short growing season (1 Oct - 28/29 Feb)	350	404	773	381	628	317	-
Dry Season (1 Aug - 30 Sept)	9	16	2	4	8	11	-
Annual total	782	653	675	799	810	666	-

Data courtesy of Dr N Jackson, Institute of Hydrology

* Data for 9 year period (1963-1971) from Machakos Maruba Dam Station.

Table 2.2 Seasonal daily mean values and associated standard errors for mean, maximum and minimum air temperature, incident solar radiation, daytime atmospheric vapour pressure deficit (SD) and relative humidity at 0700 and 1400 h, and potential evapotranspiration for each experimental season. Seasonal total values for evapotranspiration and rainfall are also shown. Measurements were recorded using an automatic weather station located 2 m above the tree canopy.

Season	Air temperature (°C)			Solar radiation ($MJ\ m^{-2}\ d^{-1}$)	SD (kPa)	Relative humidity (%)			Potential evapotranspiration ($mm\ d^{-1}$)	Rainfall (mm)
	Mean	Maximum	Minimum	Mean	Daytime mean (0700-1900)	Daytime mean (0700-1900)	700	1400	Mean	Total
L94	19.7 +/- 0.13	24.4 +/- 0.17	15.5 +/- 0.20	17.8 +/- 0.40	0.8 +/- 0.05	68.3 +/- 0.84	41.7 +/- 2.59	58.2 +/- 0.93	2.3 +/- 0.07	356.6	200.0
D94	18.6 +/- 0.17	23.5 +/- 0.30	14.1 +/- 0.19	15.5 +/- 0.76	0.7 +/- 0.04	66.4 +/- 0.99	92.6 +/- 0.62	58.6 +/- 1.22	2.5 +/- 0.13	152.2	8.2
S94/95	20.1 +/- 0.08	25.1 +/- 0.17	15.6 +/- 0.12	20.4 +/- 0.31	1.2 +/- 0.04	76.0 +/- 0.83	92.7 +/- 0.30	68.6 +/- 0.99	3.9 +/- 0.06	548.7	627.3
L95	19.3 +/- 0.11	24.2 +/- 0.17	15.1 +/- 0.19	16.4 +/- 0.39	0.8 +/- 0.02	71.9 +/- 0.66	96.9 +/- 0.27	63.7 +/- 0.88	3.0 +/- 0.08	452.0	302.5
D95	18.7 +/- 0.14	24.0 +/- 0.28	13.9 +/- 0.24	16.3 +/- 0.74	0.9 +/- 0.04	65.9 +/- 1.06	95.8 +/- 0.43	57.6 +/- 1.44	2.7 +/- 0.13	163.9	10.5
S95/96	21.2 +/- 0.15	26.8 +/- 0.21	16.4 +/- 0.16	20.8 +/- 0.28	0.9 +/- 0.02	73.2 +/- 0.61	66.9 +/- 3.35	50.6 +/- 1.76	2.9 +/- 0.14	438.0	321.1

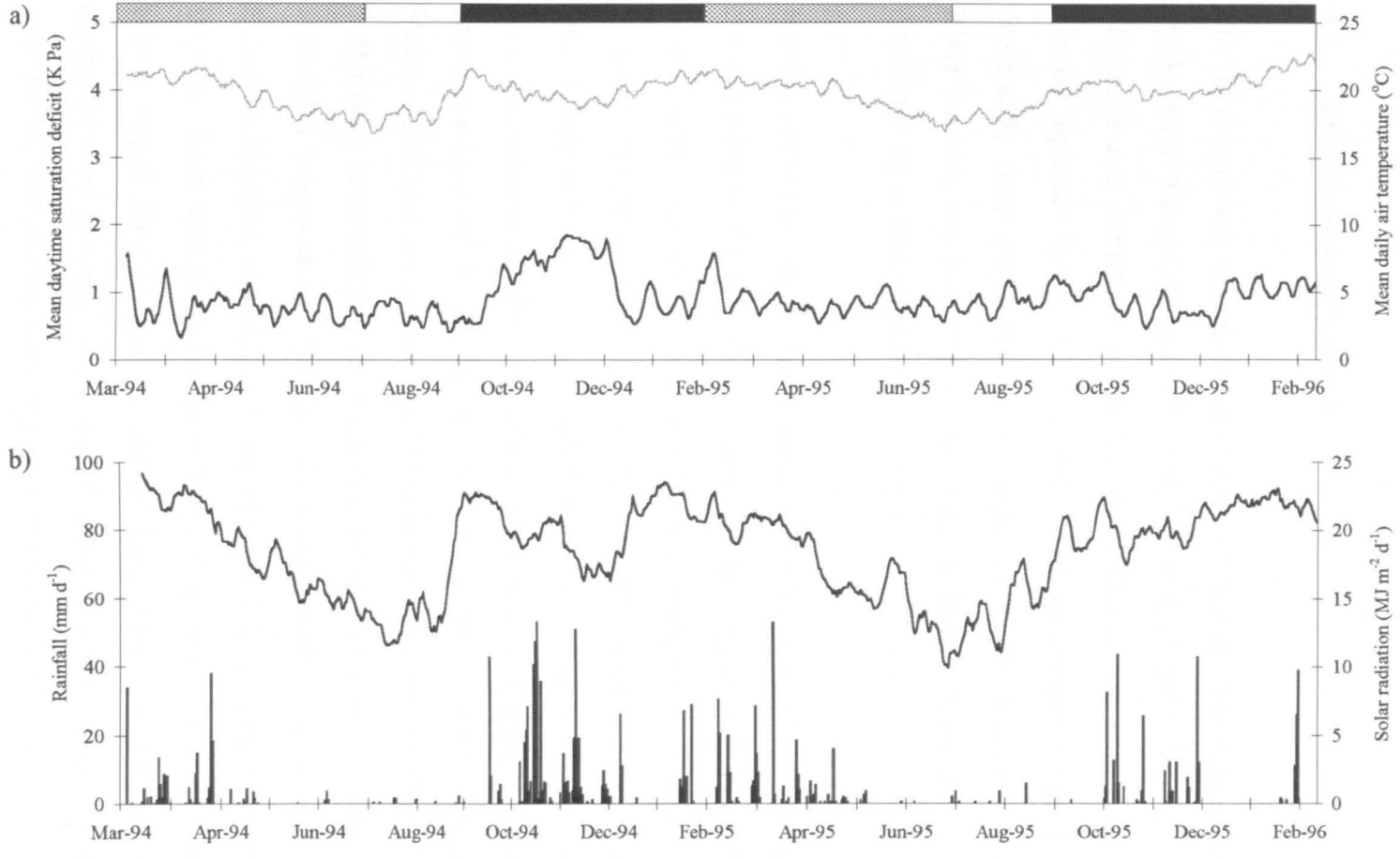


Figure 2.1 Timecourses for a) mean daytime (0700 to 1900 h) saturation deficit (black line) and mean daily (0100 to 2400 h) air temperature (grey line) and b) total daily shortwave radiation (black line) and daily rainfall (columns) for the CIRUS site during the final four experimental seasons; long growing 1994 to short growing season 1995/96. The horizontal bars represent seasons; black, short growing season (Oct-Feb); grey, long growing season (Mar-Jul); and open, dry season (Aug-Sep).

CHAPTER 2

MATERIALS AND METHODS

2.1 LOCATION AND CLIMATE

The field work was carried out at ICRAF's Machakos Field Research Station, 80 km south-east of Nairobi, Kenya (1E 33' S, 37E 8' E, altitude 1560 m; Kibe *et al.*, 1981). The soils and climate at Machakos Field Station are typical of the surrounding Kenyan uplands (Scott *et al.*, 1971). The experimental site was located on a moderately steep south-west facing slope (18-22 %) leading down to the Maruba River terraces, and had no previous cropping history before being cleared of scrub dominated by Acacia species in July 1991.

Rainfall distribution in the Machakos region is bimodal, with the short rains extending from October to the end of December and the long rains from March to the end of May. These rainy seasons correspond to the short growing season (S) which extends from c. 1 October to 28/29 February, the long growing season (L) between c. 1 March and 31 July and the dry season (D) between c. 1 August and 30 September (Table 2.1). Each season is defined according to the year in which it occurred; thus the short growing season of 1993/94 is identified as S93/94. Rainfall is typically greatest in March, April and November, with little or no rain being received between July and September. Mean rainfall receipts during the short and long growing seasons between 1963-1971 were 414 and 359 mm respectively, with an annual average of 782 mm. However, monthly, seasonal and annual rainfall is extremely variable in Machakos District. Thus, during the five year duration of the trial, rainfall during the growing season ranged from 112 mm during the long growing season of 1993 to 773 mm during the short growing season of 1992/93; the variation in annual rainfall during the same period was smaller, ranging from 651 mm in 1991 to 811 mm in 1994. Potential evaporation varies between 95 and 165 mm $month^{-1}$, giving an annual total of c. 1450 mm (Huxley *et al.*, 1989). Air temperatures are relatively cool and daytime atmospheric humidity is relatively low.

The seasonal climatic conditions experienced during the final four rainy seasons and the corresponding dry seasons were measured using an automatic weather station located 2 m above the tree canopy and are summarised in Table 2.2 and Figure 2.1. The short growing season provides the most extreme conditions during the annual cycle, with the highest maximum air temperatures, relative humidities, rainfall and potential evapotranspiration. In all seasons except S94/95, potential seasonal evapotranspiration exceeded total seasonal rainfall. A detailed climatic description for Machakos District is given by Huxley *et al.* (1989).

2.2 EXPERIMENTAL DESIGN

CIRUS was designed to investigate the influence of competition and the extent of complementarity between *Grevillea robusta* and associated crops for above and below-ground resources. The main trial comprised a balanced incomplete block design containing five treatments replicated four times, together with an extra five sole crop plots (Fig. 2.2 and Plate 2.1). Plot size was approximately 22 x 22 m, which provided an experimental area of 18 x 18 m in the centre of each plot free from the effects of inter-plot interference. Crops were planted at a spacing of 33 x 100 cm for maize (3030 plants ha^{-1}) and 15 x 50 cm for cowpea (13333 plants ha^{-1}). The five treatments are illustrated in Figure 2.3 and described below:

- Cg: sole maize (*Zea mays* (L.); Katumani composite) or cowpea (*Vigna unguiculata* (L.) Walp.).

- CTd: dispersed trees with crops; trees planted at a 3 x 4 m spacing, 35 trees per plot (833 trees ha^{-1}).

- CTc: contour-planted tree rows with crops; tree spacing 2 x 9 m, 30 trees per plot (640 trees ha^{-1}).

- CTa: across-contour planted tree rows (up-and-down slope) with crops; tree spacing 2 x 9 m, 30 trees per plot (640 trees ha^{-1}).

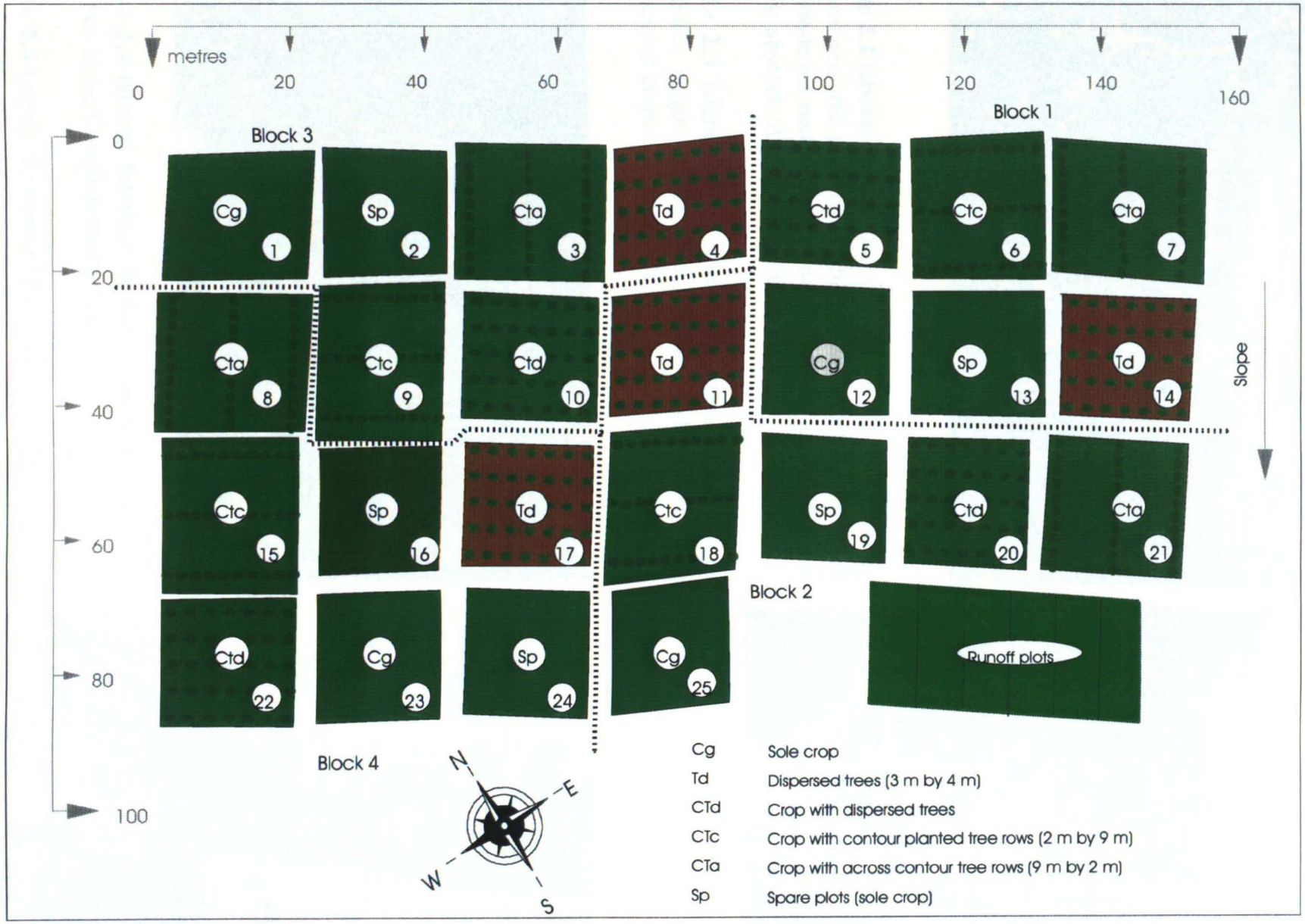


Figure 2.2 Experimental layout for CIRUS. The rhomboidal shape of some plots is due to the contour planting of the tree rows and the extension of plot edges adjacent to tree rows (courtesy of S.B. Howard).

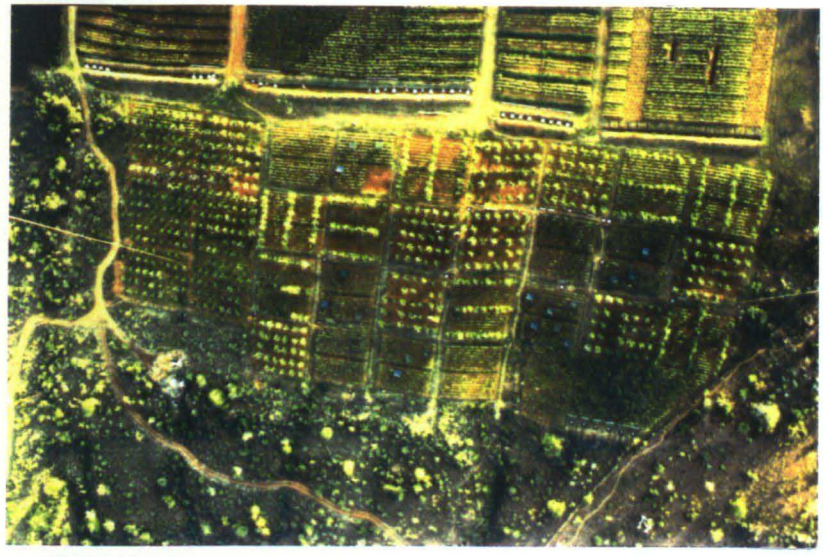


Plate 2.1 (above) Aerial view of main CIRUS trial showing the various tree planting arrangements, sole crop plots and the shade net enclosures used to examine the impact of shade in the absence of tree competition.

Plate 2.3 (right) Basal pruning of grevillea canopy to produce single trunks and control competition with associated crops.

Plate 2.2 (above) Interface between grevillea, maize and cowpea in the Complementary Trial.

Plate 2.4 (right) Extensive basal damage to the trunks of grevillea by termites.

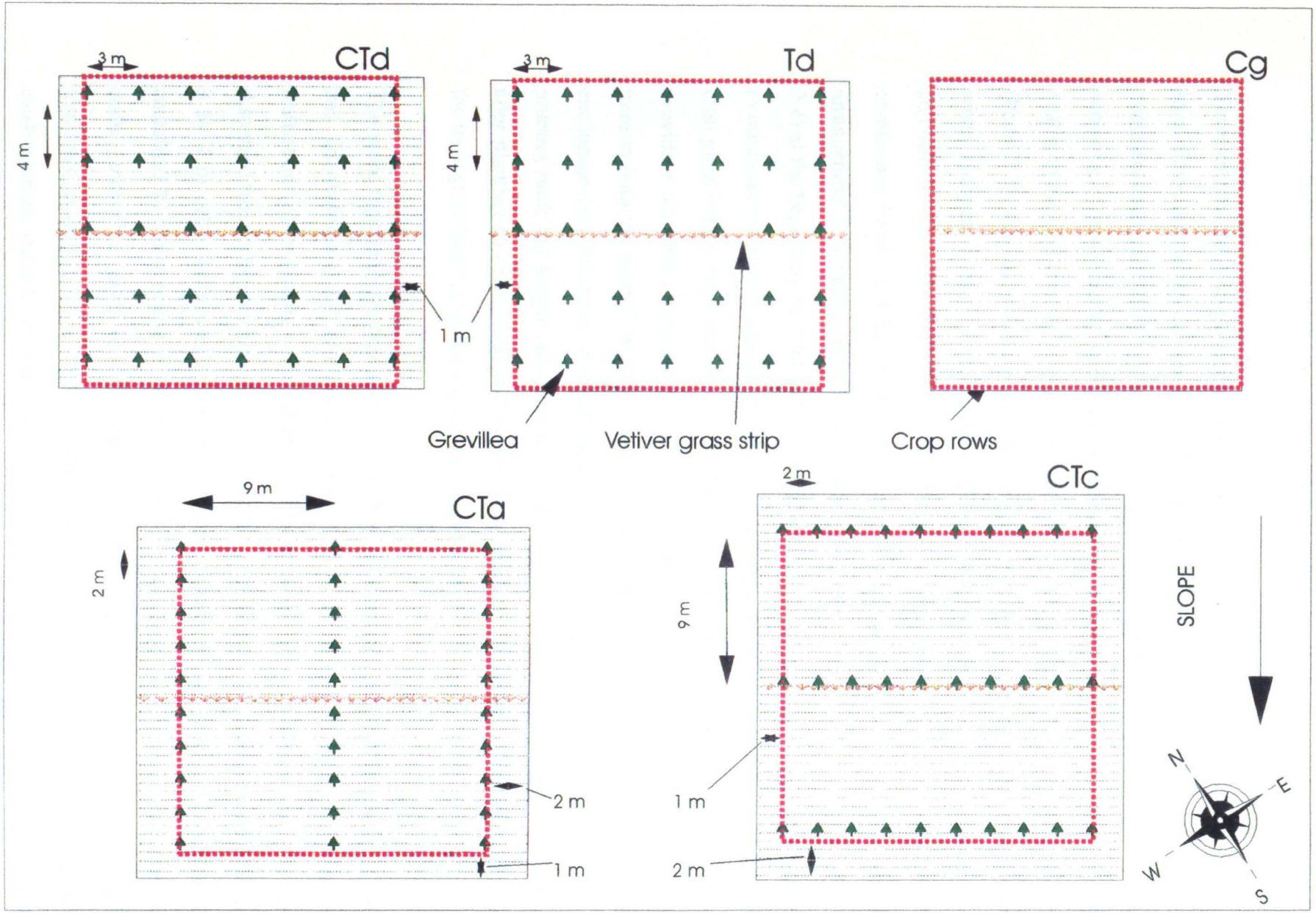


Figure 2.3 Plot layouts of treatments in CIRUS; the red dashed squares indicate the 18 x 18 m size of the sole crop plots for comparison (courtesy of S.B. Howard).

- Td: dispersed sole trees planted at 3 x 4 m spacing, 35 trees per plot (833 trees ha^{-1}).

Three month old, pot-grown tree seedlings of *Grevillea robusta* (A. Cunn. ex R. Br., local Embu provenance) were planted in the main trial (1.6 ha) in October 1991. A complementary site (0.6 ha) was cleared and planted in 1992 to permit destructive sampling of grevillea for validation of allometric growth analysis procedures and to enable maize and cowpea to be grown concurrently rather than in consecutive seasons (Plate 2.2), thereby avoiding inter-seasonal variability in environmental conditions when comparing crop performance. The Complementary trial was immediately adjacent to the main CIRUS trial (cf. Plate 2.1) and contained trees planted in a continuous block (0.4 ha) at a density and distribution identical to the dispersed arrangement in the main trial (3 x 4 m). This block was sub-divided into 8 plots (Fig. 2.4) at the beginning of L94 and a seasonal rotation of cowpea and maize was grown to minimise the risk of disease transfer between consecutive cowpea crops. Five sole crop plots with a combined area of 0.2 ha were cleared in August 1994 (Fig. 2.4) to provide a seasonal rotation of maize and cowpea in the complementary trial. The trees in both the main CIRUS trial and the Complementary trial site were managed to encourage the production of single stems and maintain a uniform canopy structure by pruning back the longer side-branches at the first pruning approximately two years after planting (6 June 1993) and by removing the lower branches (basal pruning) as the trees grew taller at all subsequent prunings (Plate 2.3).

The work reported here concentrates primarily on measurements within the Cg, CTd and Td treatments and specifically within plots 4, 5, 12 and 13 (Fig. 2.2) due to restrictions on sampling imposed by the limited availability of equipment. In the dispersed tree arrangements (Td and CTd), the plots were subdivided into individual 3 by 4 m cells, delineated by the tree located at each corner (Fig. 2.3); each cell contained 40 maize plants or 144 cowpea plants and was given a unique identification code. Individual plots were separated by grass walkways to facilitate access and minimise erosion. As a further erosion control measure, particularly during the establishment period, vetiver grass (*Vetiveria zizanoides* (L.) Nash) strips were contour-planted across the centre of each plot (Fig. 2.3); the trees and crops were

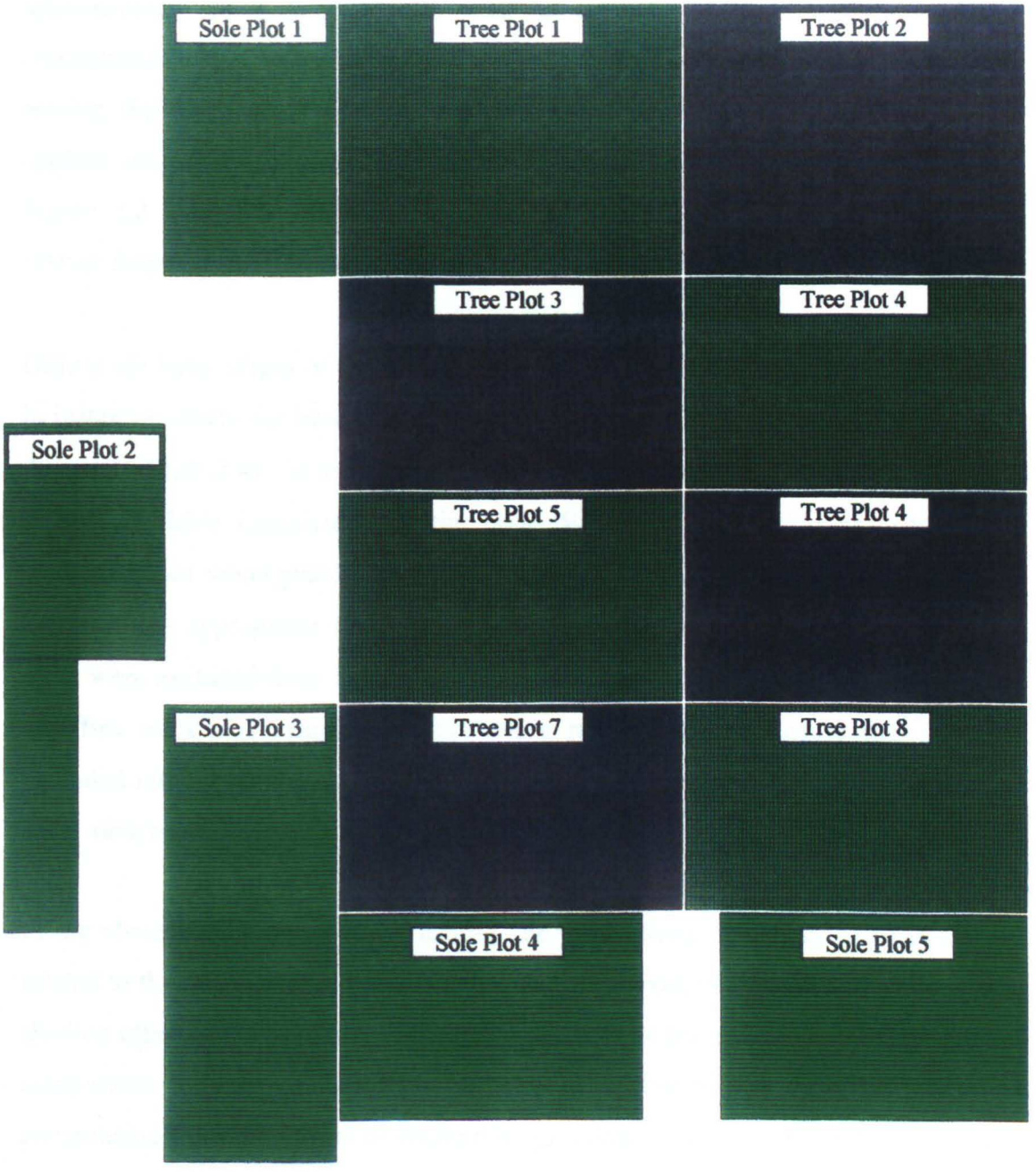


Figure 2.4 Layout of the five sole crop (Sole Plot 1-5) and eight agroforestry plots (Tree Plot 1-8) within the complementary site. The agroforestry plots were divided into two sets of four (illustrated by the shading) to allow maize and cowpea to be grown concurrently; crops were rotated seasonally within each set.

planted parallel to these strips. The walkways and vetiver strips were cut at approximately 14 d intervals, the latter to a height of 10-15 cm, to minimise competition with adjacent trees and crops. The plots were hand-weeded before sowing the crop and as required during the growing season. No fertilisers were applied and no residues were incorporated into the soil. The runoff plots shown in Figure 2.2 were established in September 1993 to determine the influence of the vetiver strips on runoff, erosion and crop growth.

During the latter stages of the trial, termite attack damaged some trees, causing death in instances where the bark and sapwood were removed in a continuous ring around the trunk (Plate 2.4). In such cases, the trees and surrounding soil were treated with locally available insecticide and the basal 50 cm of the trunk was coated with creosote-based wood preservative twice per year. Trees that died were replaced to maintain the appropriate spatial arrangement, but these and surrounding cropping areas were excluded from further experimental observations. The lateral extension of grevillea roots was examined before every rainy season to ensure they had not extended into adjacent plots and, where necessary, trenching techniques were used to sever such roots.

In the absence of limiting stress factors, the productivity of annual crops is closely related to the quantity of radiation intercepted. However, in agroforestry systems, the shading effect of the trees on understorey crops may be compounded by below-ground competition for water and nutrients. In order to separate the impact of below-ground competition from the effects of shading by grevillea, sections of the sole maize plots were covered with spectrally neutral shade netting (Lowes of Dundee, U.K.) which removed 25, 50 or 75 % of the incident radiation. The netting was attached to 3 x 4 m steel frames (Plate 2.5), equivalent to the size of individual cells in the Td and CTd treatments. The stands were height-adjustable to allow for crop growth. 3 x 4 m non-shaded areas or cells within the sole crop plots were also demarcated at the beginning of the season to enable comparison of shaded and unshaded sole crops (Plate 2.6). Sole crops grown under shade nets are defined as Cg 25%, Cg 50% and Cg 75% depending on the percentage of incident radiation removed in each treatment, while the non-shaded sole crop cells are referred to as Cg 0%.

Plate 2.5 Shade net cages allowed the effects of shade to be examined in the absence of competition from trees; the height-adjustable cages provided 25, 50 or 75% neutral shade.

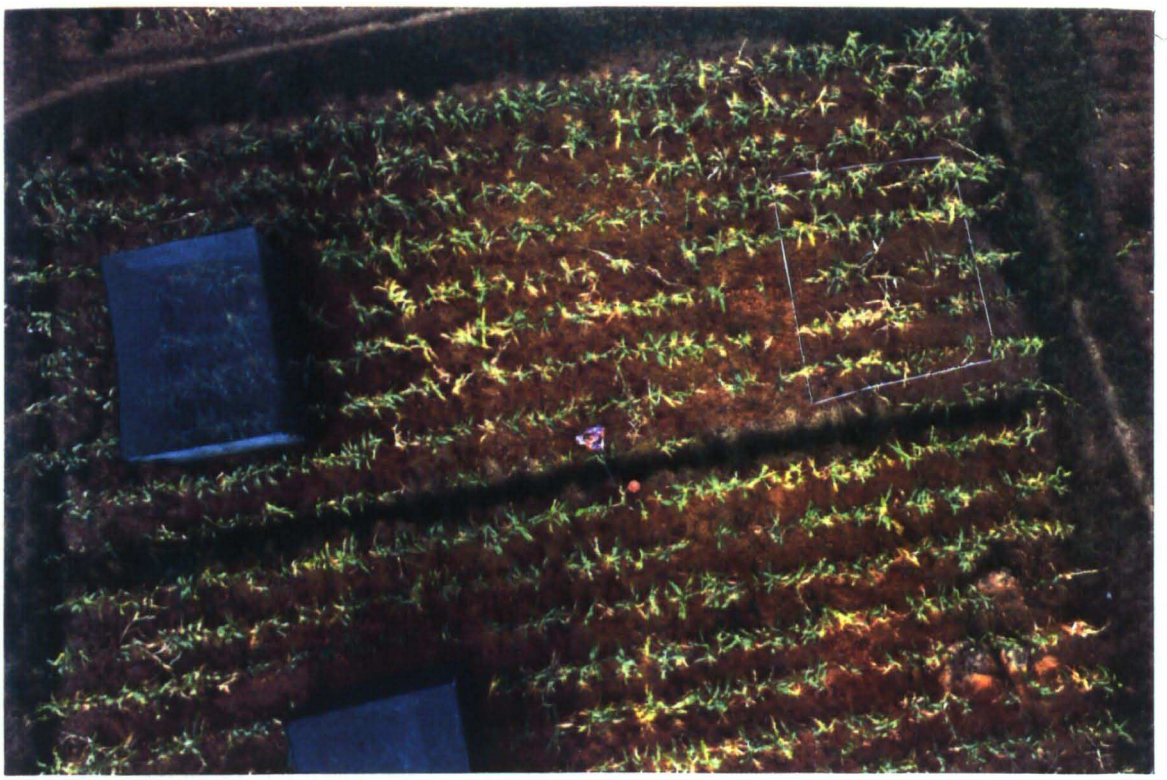


Plate 2.6 Aerial view of sole maize showing shade net cages and a defined unshaded control (Cg0%) area (top right).

2.3 SOIL CHARACTERISTICS

The soil was a well-drained, shallow to moderately deep (0-2.5 m) sandy clay loam characterised as a Khandic Rhodustalf overlying petroplinthite (murram), and was stony with gravel bands. Soil pits excavated in April 1993 demonstrated the presence of five distinct horizons, with the uppermost stone-free layer being further sub-divided into till (0-0.4 m), sub-surface (0.4-0.8 m) and clay (0.8-1.0 m) layers. Analysis of soil physical characteristics by the Institute of Hydrology indicated that bulk density and particle density increased with depth, from 1.19 and 2.49 g cm^{-3} respectively in the surface horizon to 1.67 and 2.62 g cm^{-3} respectively for the eroded bedrock; all soil horizons had moisture retention (pF) characteristics typical of sandy or sandy clay soils. Further details of soil physical properties are given by Wallace *et al.* (1995). Analyses carried out in an adjoining trial (Kiepe, 1995) indicated that the soil was not nutrient-limiting for crop growth, containing moderate levels of phosphate (4-7 mg kg^{-1}) and nitrogen and had a soil organic carbon content of 1 %.

Soil analyses were carried out in May 1996 to assess the effects of the treatments imposed on soil nutrient status in the main CIRUS trial using Kiepe's (1995) survey as a benchmark. Soil samples were collected to a depth of 30 cm using an auger as follows:

- Sole crop (Cg): soil cores were taken at 8 randomly selected sites in all four replicates; cores from each plot were bulked prior to analysis.

- Sole tree (Td) and dispersed agroforestry treatments (CTd): soil cores were taken 50 and 250 cm from eight randomly selected trees in all four replicate plots; four of the 50 cm samples were located upslope and four downslope from the tree. The 250 cm samples were taken from the centre of the cell bounded by four neighbouring trees. All samples were bulked according to distance from the tree to provide four replicates per plot at distances of 50 and 250 cm from trees in the Td and CTd treatments.

The soil samples were analysed for pH, ammonium, nitrate and available phosphorus, calcium, magnesium, potassium and total organic carbon. K and P were extracted using a modified Olsen technique, with K concentration being determined by flame photometry and P by colorimetry using the molybdenum blue method, while Ca and Mg were extracted using 1N HCl and analysed using atomic absorption spectrometry (AAS). Soil organic carbon was oxidised using a modified Medius method and determined colorimetrically; inorganic nitrogen was extracted using 2N KCl (Lott *et al.*, 1997).

Soil chemical attributes did not differ significantly between treatments, with two exceptions (Fig. 2.5). Soil NH_4^+ and NO_3^- concentrations were significantly higher in the sole crop plots (Cg) than in the agroforestry plots (Td and CTd; $p<0.01$-0.05), whereas the converse applied for soil P, whose concentration was significantly lower in the Cg plots than in either the CTd ($p<0.05$) or Td ($p<0.01$) treatments. Previous research has suggested that the cluster roots of grevillea may increase available P by solubilising soil phosphates at depth (Skene *et al.*, 1996). Their view was apparently supported by the higher soil phosphate status within the agroforestry treatments and the significantly higher concentrations of total P in maize within the CTd treatment (Fig. 2.6; $p<0.01$). The apparent decline in soil nitrogen in the CTd and Td treatments may reflect the increased demand resulting from the rapid growth and high productivity of the trees. Soil nitrogen content did not differ significantly between locations close to or more distant from the trees in the Td treatment, whereas NH_4^+ was higher and NO_3^- was lower adjacent to the trees in the CTd treatment ($p<0.01$); the origin of this difference is unclear and was not supported by the plant analyses. Percentage nitrogen content within the above-ground biomass of maize (Fig. 2.6) was lower than that recorded by Pilbeam *et al.* (1995) for maize of the same cultivar growing at a nearby site (2.9 *vs.* 3.9 %). This was possibly because the measurements were made later in the season in CIRUS and would therefore have been influenced by loss of nitrogen during reproductive growth (Pate and Farquhar, 1988). None of the nutrient concentrations or other soil variables examined were at limiting levels for maize growth (Smithson, pers. comm.), although Torquebiau (in ICRAF, 1994) demonstrated that yields could be increased to the maximum reported for this maize cultivar under the prevailing soil and climatic conditions at Machakos Field Station by

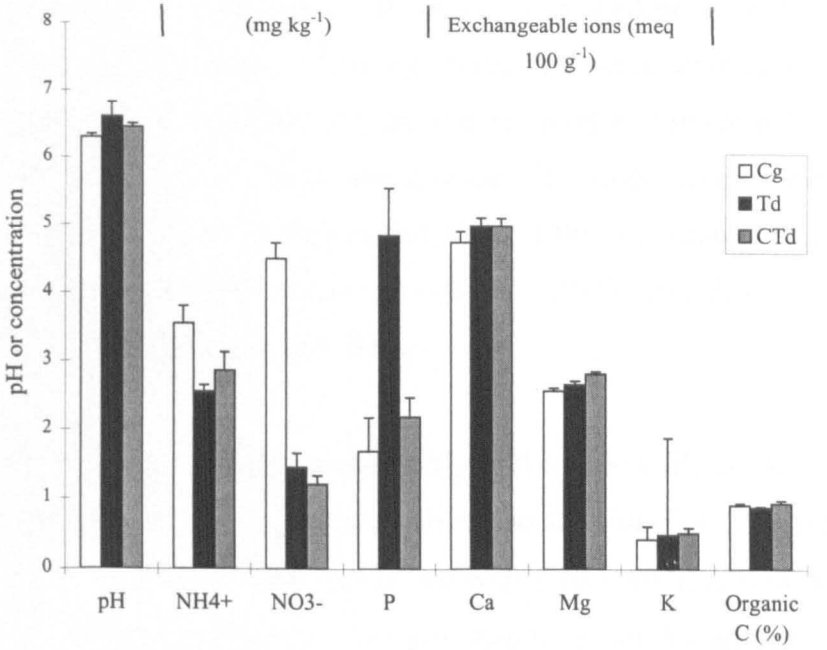


Figure 2.5 Analysis of soil pH and nutrient concentrations in sole maize (Cg), sole tree (Td) and the dispersed agroforestry (CTd) treatments during the short growing season 1995/96. Single standard errors of the mean are shown.

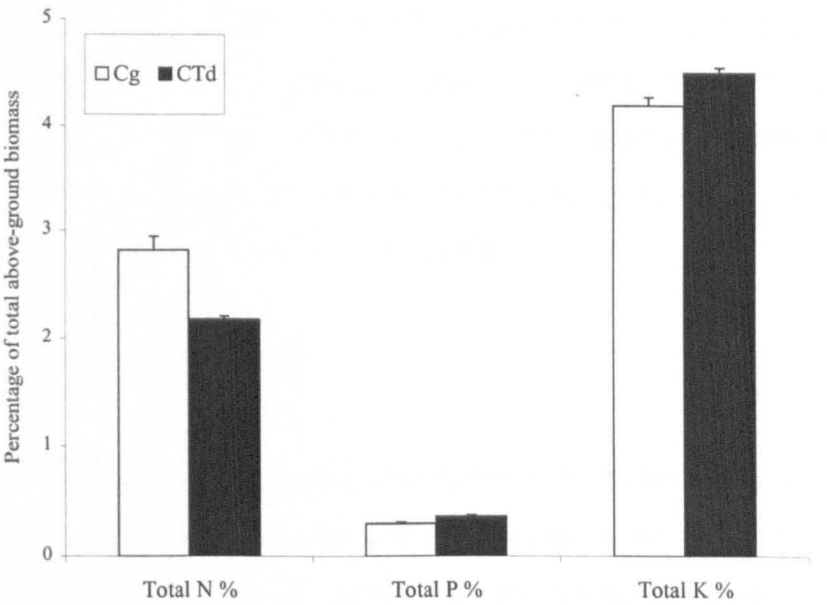


Figure 2.6 Nutrient analysis of the aboveground biomass of maize in sole (Cg) and agroforestry (CTd) treatments sampled at approximately the time of maximum growth rate during the short growing season 1995/96. Single standard errors of the mean are shown.

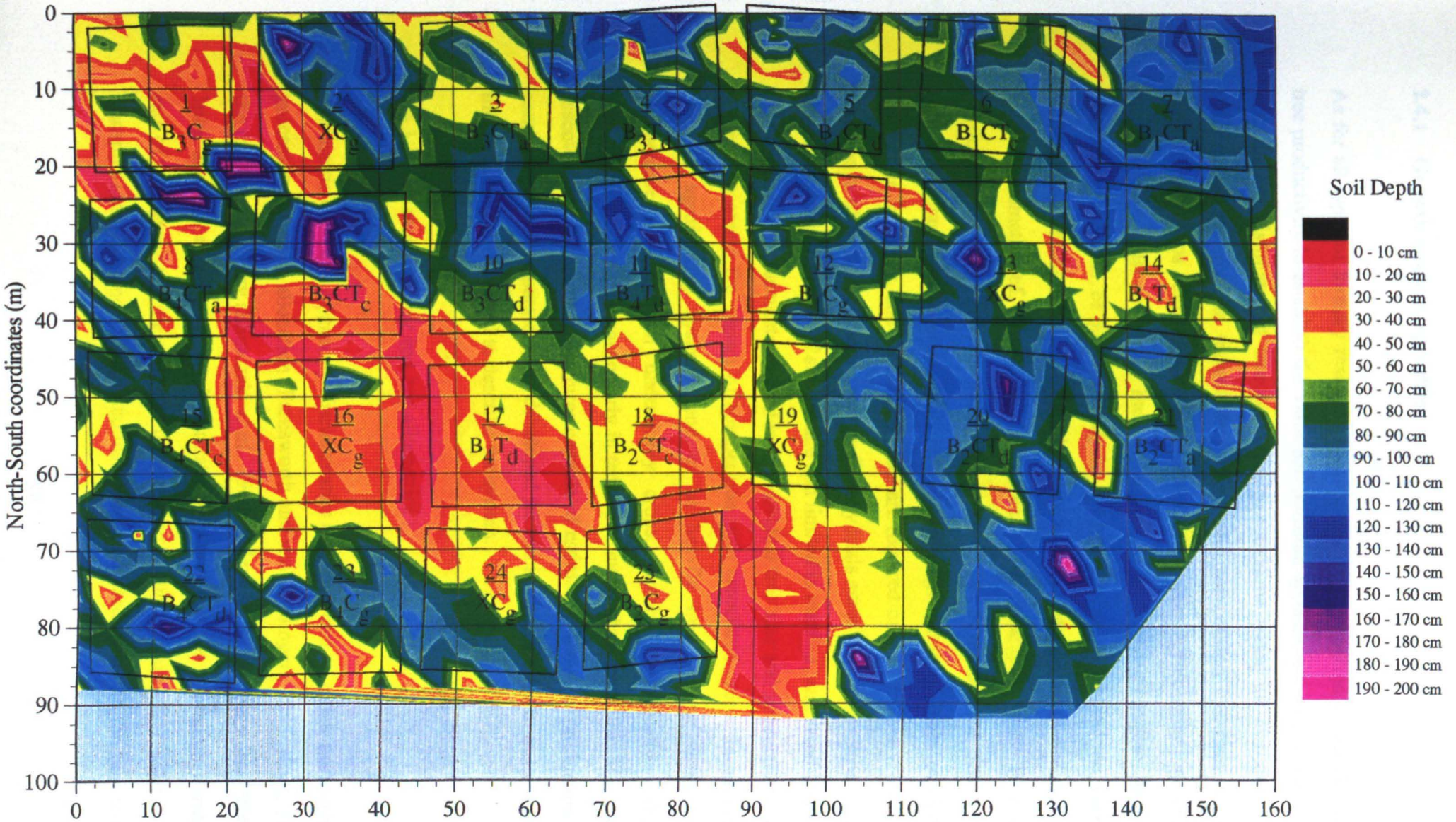
applying NPK fertiliser and irrigation. However, it is unclear from his analysis whether nutrients were the primary limiting factor for maize growth at this site. Pilbeam and Warren (1995) suggested that the low recovery of applied N fertiliser by maize and beans on a nearby site was a consequence of the high rate of mineralisation at the onset of the rains which supplied almost 70 % of the high crop N-requirement. Thus it remains most likely that plant growth in CIRUS was limited by water availability rather than a shortage of nutrients.

Soil depth above the bedrock varied considerably in the main CIRUS trial, as shown by a survey conducted at 4 x 4 m grid intervals across the site (Fig. 2.7) in February 1993 (Howard, 1997). The site was marked out with a 40 x 40 m grid on which the positions of the plots were recorded. This grid was then sub-divided into 4 x 4 m squares and a 5 cm diameter auger was used to determine soil depth at the corners of each square. If this differed markedly from neighbouring sampling points, an additional measurement was made 20-30 cm away to reduce the risk of underestimating the true soil depth due to the presence of erratic stones within the profile. Further points were added during the installation of neutron probe access tubes (June-October 1993). Figure 2.7 clearly indicates that an area of shallow soil (0.2-0.6 m) traversed the site between the upper north-west corner and the lower south-east corner, with soil depth generally being greater above and below this band. Additional soil depth measurements were carried out in the complementary site using a 1.5 x 2.0 m grid in August 1994 (Lott *et al.*, 1997).

2.4 GROWTH AND DEVELOPMENT

It was important to establish reliable non-destructive methods for determining standing biomass and leaf area in maize and grevillea since the relatively small plot size and low plant populations precluded frequent destructive sampling. Such information was essential if resource use efficiencies were to be calculated reliably from concurrent measurements of light interception and water use.

Figure 2.7 Soil depth map of the CIRUS site. The depth of the soil was recorded on a 4m by 4m grid covering the entire site and the data were interpolated between these points to produce the graph (courtesy of N.A. Jackson)



C_g Crop plots (without trees)

T_d Tree plots (without crop) in dispersed (3m x 4m) arrangement

CT_d Crop plots + trees in dispersed (3m x 4m) arrangement

CT_c Crop plots + trees following contours; (9m x 2m arrangement)

CT_a Crop plots + trees across contours (downslope - 9m x 2m arrangement)

2.4.1 Growth analysis - grevillea

As for all types of forestry research, agroforestry requires periodic measurements of tree productivity to establish the value and potential applicability of the system under examination. Estimates of tree productivity should be based on methods that are sufficiently sensitive to detect the effects of competition between trees and understorey crops throughout the life-cycle of the agroforestry system but, paradoxically, must involve a limited number of destructive samples. Most non-destructive methods of growth analysis for tree species are based on regression models which relate biomass or productivity to some non-destructively measurable growth parameter (cf. Whittaker and Marks, 1975; Natarajan, 1988; Fownes and Harrington, 1990). In general, these models have been developed for closed canopy natural or plantation forests which have a wide age range of trees available for destructive sampling, and where estimates are required only at the stand level. This situation is often not applicable to agroforestry trials since the canopy tends not to be closed, the trees are often of similar age and limited in number, and stand level means cannot provide the accurate estimates of individual tree size and productivity that are required to assess the impact of competition with associated crops. In addition, the trees in agroforestry systems tend to be heavily managed to minimise their competitive influence on understorey crops, thereby periodically influencing allometric relationships, particularly in terms of canopy characteristics. It is therefore essential that allometric procedures capable of estimating biomass production by the canopy and trunk separately, are developed for use in agroforestry in order to provide the level of detail required to describe the system.

2.4.1.1 Pipe model theory and tree allometrics

Allometric estimates of canopy characteristics may be based on either the mechanistic processes of carbon allocation (Farnsworth and van Gardingen, 1995; King, 1996) or the pipe model theory (Shinozaki *et al.*, 1964; Valentine, 1985; Rennolls, 1994). The latter assumes a species-dependent relationship between the maximum transpiration rate of the canopy and the ability of the sapwood to conduct sufficient water to sustain transpirational demand. This relationship may be used to relate the leaf area from

which transpiration is occurring to the cross-sectional area of sapwood in the subtending branch or trunk, and is supported by considerable experimental evidence (e.g. Waring *et al.*, 1982; Chapman and Gower, 1991; Nygren *et al.*, 1993; Mencuccini and Grace, 1995). Nygren *et al.* (1993) suggested that allometric relationships based on the pipe model theory may be compromised in agroforestry systems because pruning not only reduces leaf area but may also induce the premature transformation of sapwood to heartwood, thereby altering the functional relationship between leaf area and trunk cross-sectional area (CSA). They nevertheless showed that canopy biomass (LM) and leaf area (LA) may be estimated reliably from the sum of branch diameters for re-growth branches in systems where whole-canopy pruning is practised.

Many agroforestry systems do not involve whole canopy pruning, but instead undergo partial pruning whereby whole branches are progressively removed from the base of the canopy to limit competition with understorey crops and encourage the production of poles. In such systems, the morphology of the remaining branches is unaffected, with the result that allometric relationships established between LM or LA and CSA may remain valid. However, an allometric approach based on branch measurements was inappropriate for the relatively large trees in CIRUS, which were up to 8 m tall and had up to 40 branches per tree by the end of the trial. At best, a trained team of three could measure a maximum of 10 trees per day; as the trial contained over 600 trees, this approach was clearly impractical, making the adoption of a more rapid and straightforward method essential. In addition, the contribution of the trunk to total tree biomass must be included in allometric estimates of tree productivity in agroforestry systems since this is often an important economic component, yet the methods developed by foresters for estimating tree biomass frequently cannot distinguish between trunk and branches. However, Cannell (1984) developed a method based on an extensive experimental database that may be suitable for use in agroforestry.

2.4.1.2 Development of a simplified allometric method for determining total tree biomass and leaf area for grevillea

Destructive measurements were made on twelve trees that encompassed the full range of sizes present in CIRUS during August and September 1995. Tree height, height to the base of the canopy, basal trunk diameter and trunk diameter at the base of the canopy were recorded for each tree. Height was determined using a telescopic pole capable of measuring up to 10 m, and all measurements were made from ground level immediately upslope of the trunk to minimise errors. Trunk diameter immediately below each branch and the corresponding branch diameter were also determined. Cross sectional areas (CSA) were calculated from the diameter (d) measurements assuming that the trunks and branches were circular. After determining the diameter of each branch in the canopy, the branch was removed and leaf number and leaf and branch fresh weights were determined. As noted by Keane and Weetman (1987), the specific leaf area of individual leaves may vary by a factor of more than two within tree canopies. This potential source of variation was therefore quantified by sampling five leaves of differing age and size at equal distances along each branch and determining their area using a flat bed scanner (Delta-T Devices, Cambridge, U.K.).

The leaf and branch samples were oven-dried to constant weight at 70 °C. The trunk was cut into small pieces and its fresh weight recorded before being dried to determine dry weight. Drying of the wood samples was made difficult by the large quantity of material involved, the long drying time required and the limited oven capacity available. Consequently, the calculated water content of trunks varied between 14-59 %, a much greater range than would be expected from local variation in soil water availability to individual trees, suggesting inconsistent drying of samples. An alternative method was therefore adopted in which trunk dry weight was calculated from an estimate of the specific gravity of the wood (G; 469 kg m^{-3}) and the corresponding trunk volume (V_s). The value for specific gravity used in these calculations was obtained for fully dried samples of grevillea wood harvested from CIRUS (Howard, 1997) and, although lower than the value of 570 kg m^{-3} reported by Boland *et al.* (1984), is likely to be representative of grevillea grown under the prevailing environmental conditions in Machakos, Kenya.

Measurements of grevillea trunks in CIRUS demonstrated pronounced butt-swell, in which trunk cross sectional area decreased by 50 % over a 10 % increase in height above ground-level; this is approximated by the trunk profile shown in Figure 2.8 (red line). Cannell (1984) reported that the volume of trunks of similar shape to grevillea conformed closely to that of a paraboloid (Fig. 2.8, blue line) even though its profile differed from the true shape of the trunk, apparently because the paraboloid model compensated for the underestimation of the contribution of butt-swell (Fig. 2.8; a and b) by overestimating volume towards the top of the trunk (Fig. 2.8; c and d). The volume of the paraboloid (V_s) may be calculated from measurements of trunk cross sectional area at breast height (CSA_b)and total tree height scaled by a form factor of 0.5 (Cannell, 1984). This gives the relationship:

$$V_S = \frac{h_s \times CSA_b}{2} \qquad \text{Equation 2.1}$$

where h_s represents breast height (130 cm). The product of V_s and G provides an estimate of total trunk dry weight (W_s).

The data for the five leaves sampled from each branch of each tree examined were used to calculate the mean area of individual leaves (12.6 cm^2, SD 7.5 cm^2). The total leaf area for each branch was then derived by multiplying the number of leaves present by the mean leaf area. The reliability of this method is clearly demonstrated by the close relationship between the true and estimated leaf areas of individual branches from each of the trees examined (Fig. 2.9; $r^2 = 0.99$; n=12), despite the large standard deviation for mean leaf area.

The measurement of trunk cross sectional area just below the canopy (CSA_c) for the trees in CIRUS proved an excellent allometric parameter for estimating canopy biomass (Fig. 2.10a; canopy biomass = exp(1.3689 Ln CSA_c - 3.2112); $r^2 = 0.97$; n = 108) and leaf area (Fig. 2.10b; canopy leaf area = exp(1.2498 Ln CSA_c - 1.3726); r^2 = 0.92; n = 180). Although 12 trees were used to develop the relationships shown, the number of data points available for analysis was increased by repeatedly estimating

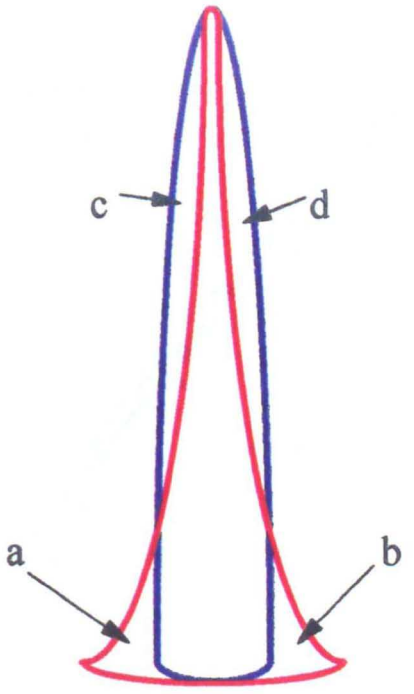


Figure 2.8 Shape of a *Grevillea robusta* trunk (red line) and the theoretical paraboloid describing trunk volume (blue line): a and b, volume of the true buttswell not represented by the paraboloid; and c and d, over-estimation of the true volume by the theoretical paraboloid.

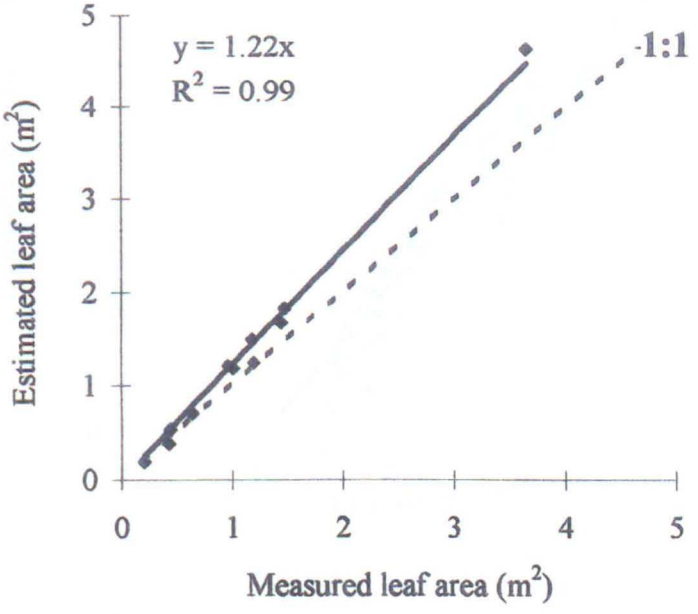
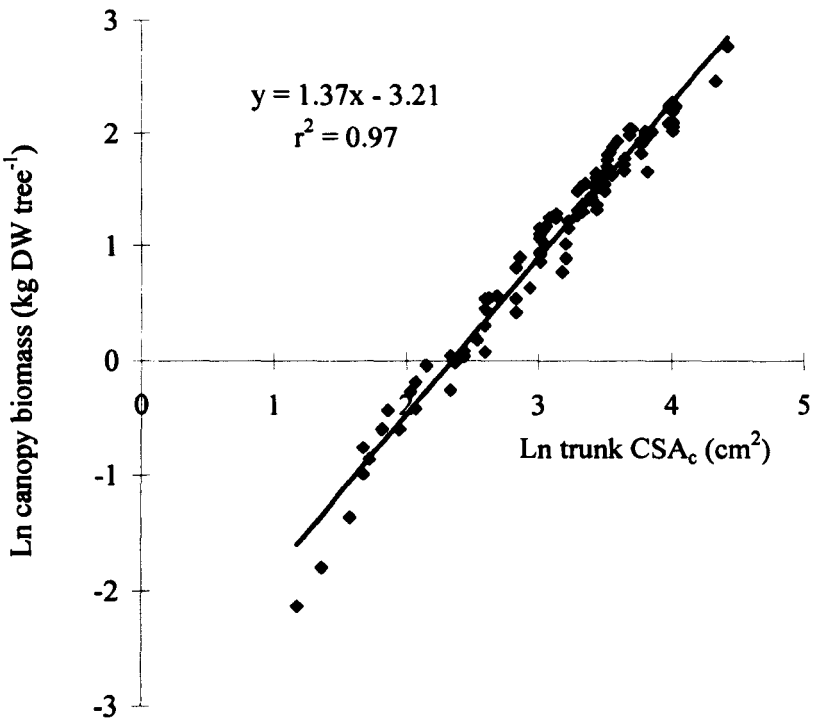


Figure 2.9 Relationship between estimated and measured leaf area of entire branches. Data are from the CIRUS site (n=12).

a)



b)

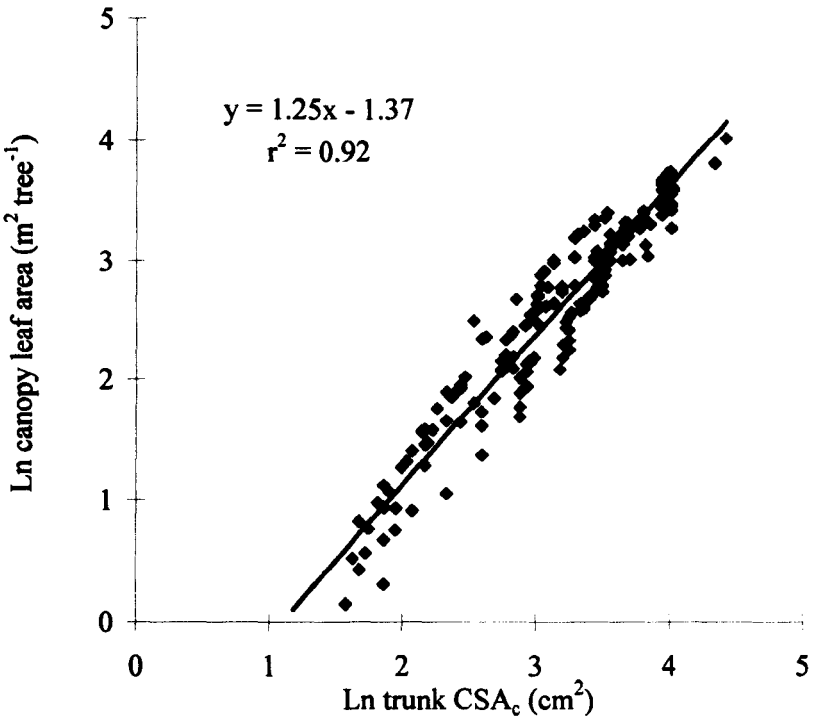


Figure 2.10 Relationship between trunk cross-sectional area and a) total canopy dry weight including leaves and branches and b) total canopy leaf area. Data are expressed as the natural log (Ln) of the observed values.

canopy size as the lower branches were removed. This approach enabled the regression to be extended to younger trees managed in a similar manner to those actually sampled, since the upper sections of the canopy corresponded to smaller crowns. The reliability of the allometric estimates of canopy biomass is apparent from the close correlation between the measured mass of material removed at each of the three prunings in CIRUS and the corresponding estimates based on trunk CSA_c (Fig. 2.11; $r^2 = 0.99$; $n = 6$). In addition, unlike estimates of canopy size derived from dimensional measurements of the branches, trunk CSA_c is capable of including the contribution of leaves which arise directly from the trunk and comprise approximately 8 % of the canopy area in grevillea. This advantage of allometric analyses based on trunk measurements contrasts with some previous studies (Margolis *et al.*, 1988; Langstrom and Hellqvist, 1991; Mencuccini and Grace, 1995) which suggested that the closest correlations were based on the summed CSA values for all branches, since the growth responses of the trunk may be delayed relative to the more dynamic responses of the leaves and branches. This was clearly not the case for grevillea when trunk cross sectional area immediately below the lowest branch was used.

The relationship between trunk dry weight (W_t), calculated as the product of trunk volume and the specific density of grevillea wood, and trunk fresh weight is shown in Figure 2.12 ($r^2 = 0.87$; $n = 12$). The slope of this regression indicates that the trunks contained approximately 52 % water at the time of sampling. This value is identical to the mean of 52 % (n=390, s.e.m.=0.5 %) previously established for branch and trunk wood of grevillea in CIRUS (Howard, 1997), indicating that the method of dry weight estimation adopted in the present study was appropriate.

2.4.1.3 Sampling regime for measuring tree growth

Allometric measurements were scheduled at monthly intervals between planting and project end, but limitations on equipment and labour availability meant that this was not always possible. At times, a compromise solution was reached, in which measurements concentrated on trees growing only in those plots where intensive measurements of water use and light interception were carried out. The parameters measured varied little during the experiment. Those measured prior to the second

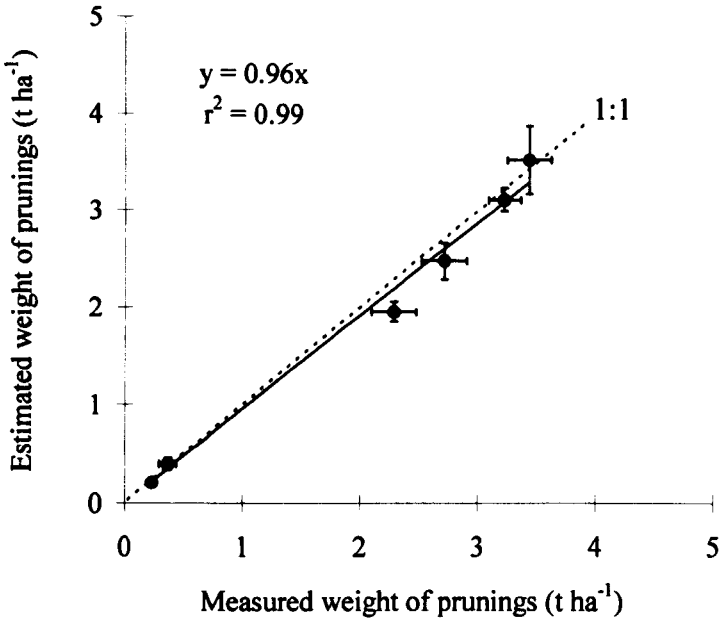


Figure 2.11 Relationship between the estimated and measured weights of canopy prunings from Grevillea robusta in CIRUS. Double standard errors of both means are shown.

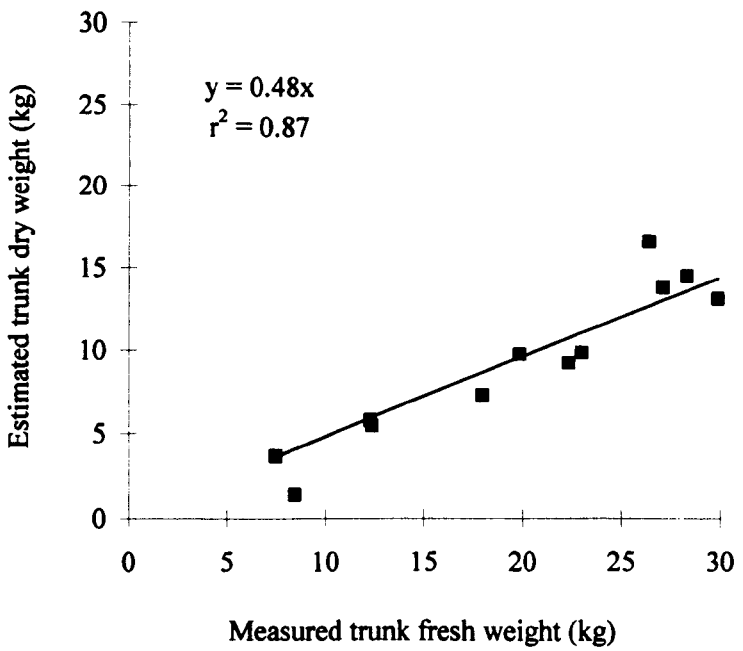


Figure 2.12 Relationship between trunk dry weight, calculated from trunk volume and specific gravity of wood, and measured trunk fresh weight.

pruning on 23 February 1994 included total height, trunk basal diameter, trunk diameter at breast height (DBH) and leaf number. After the second pruning, measurements of trunk diameter immediately below the first branch and height to the first branch (i.e. the base of the canopy) were added. Biomass was calculated using the allometric methods described above, with CSA_c being assumed to be equal to basal CSA from planting to the first pruning (DAP 0 to 599) and equal to DBH from the first to the second pruning (DAP 599 to 863). Leaf area was estimated as the product of canopy leaf number and specific leaf area (50.15 $cm^2\ g^{-1}$; Howard, 1997) up to the first pruning and thereafter was based on the allometric estimation of leaf area described in Section 2.4.1.2. The location of all diameter measurements was defined by a white line painted on trunks to ensure continuity.

2.4.2 Crop growth analysis

Growth analyses of understorey crops in agroforestry systems are subject to similar constraints to those which affect growth analysis of the associated trees (cf. Section 2.4.1). In particular, the limited number of plants and small plot size restricts destructive sampling at key points during the cropping season. As a result, non-destructive methods were developed to estimate the leaf area and above-ground biomass of crops grown during the cropping seasons. These methods were adopted during the final four experimental seasons, L94 to S95/96.

2.4.2.1 Maize: L94 to S95/96 growing seasons

Non-destructive measurements were made at regular intervals between thinning and final harvest in the CTd and Cg treatments using plants selected at thinning. The sampling locations within the CTd treatment were chosen to represent the full range of interactions between distance and direction from the trees (Figs. 2.13 and 2.14). Each position was replicated around seven trees in the CTd treatment (four trees in plot 5 and one in each of the remaining CTd plots) for each of 16-20 locations. Four maize plants were examined in each replicate shade net (Cg 25%, Cg 50% and Cg 75%) and in the unshaded sole crop treatment (Cg 0%) in positions equivalent to those used in the CTd plots (Fig. 2.15). The parameters measured during non-

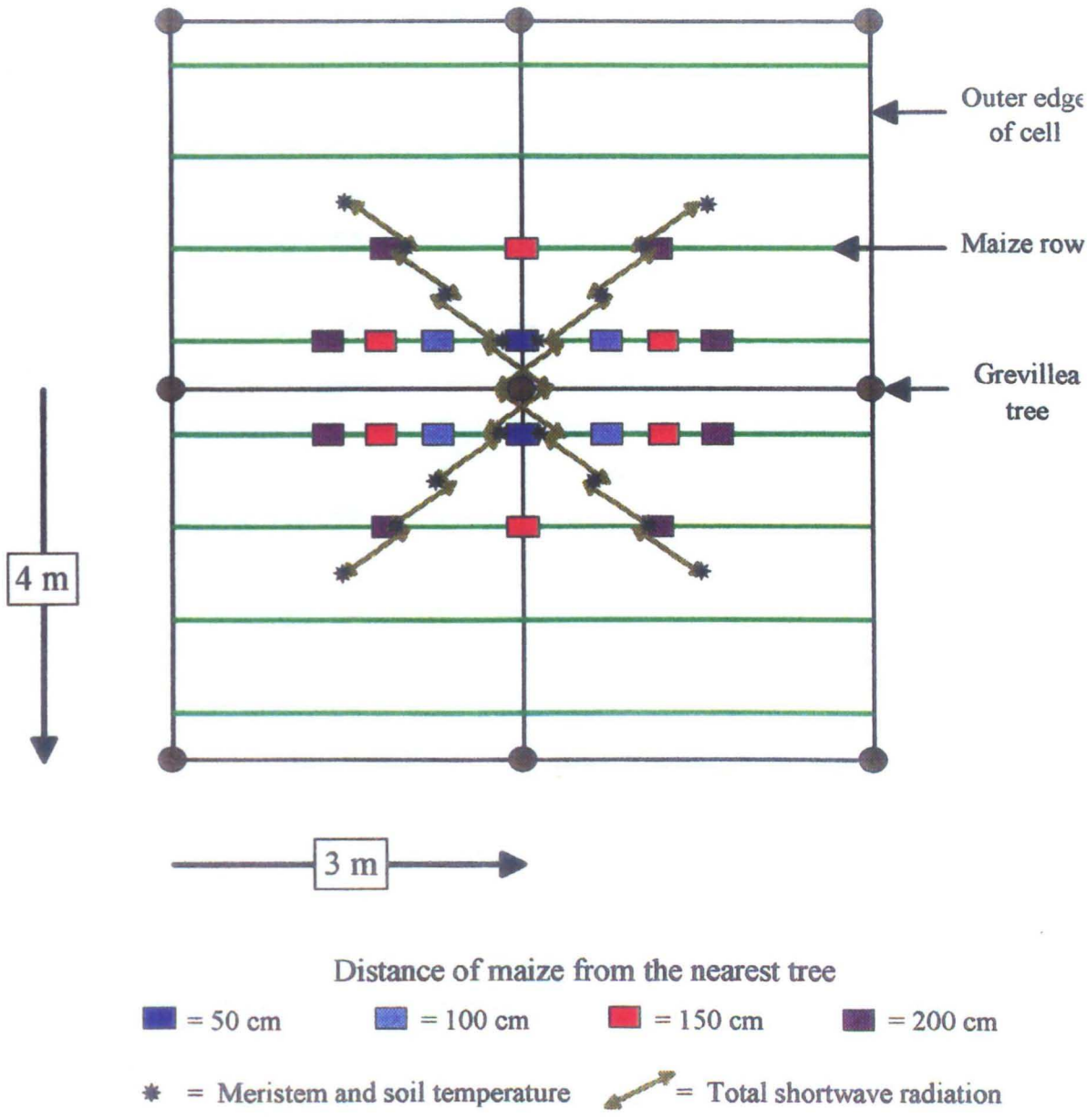


Figure 2.13 Location of intensive crop growth and development measurements in the dispersed agroforestry (CTd) plots during the 1994 long and 1994/95 short growing seasons and total shortwave radiation and meristem and soil temperature measurements during the 1994 long growing season.

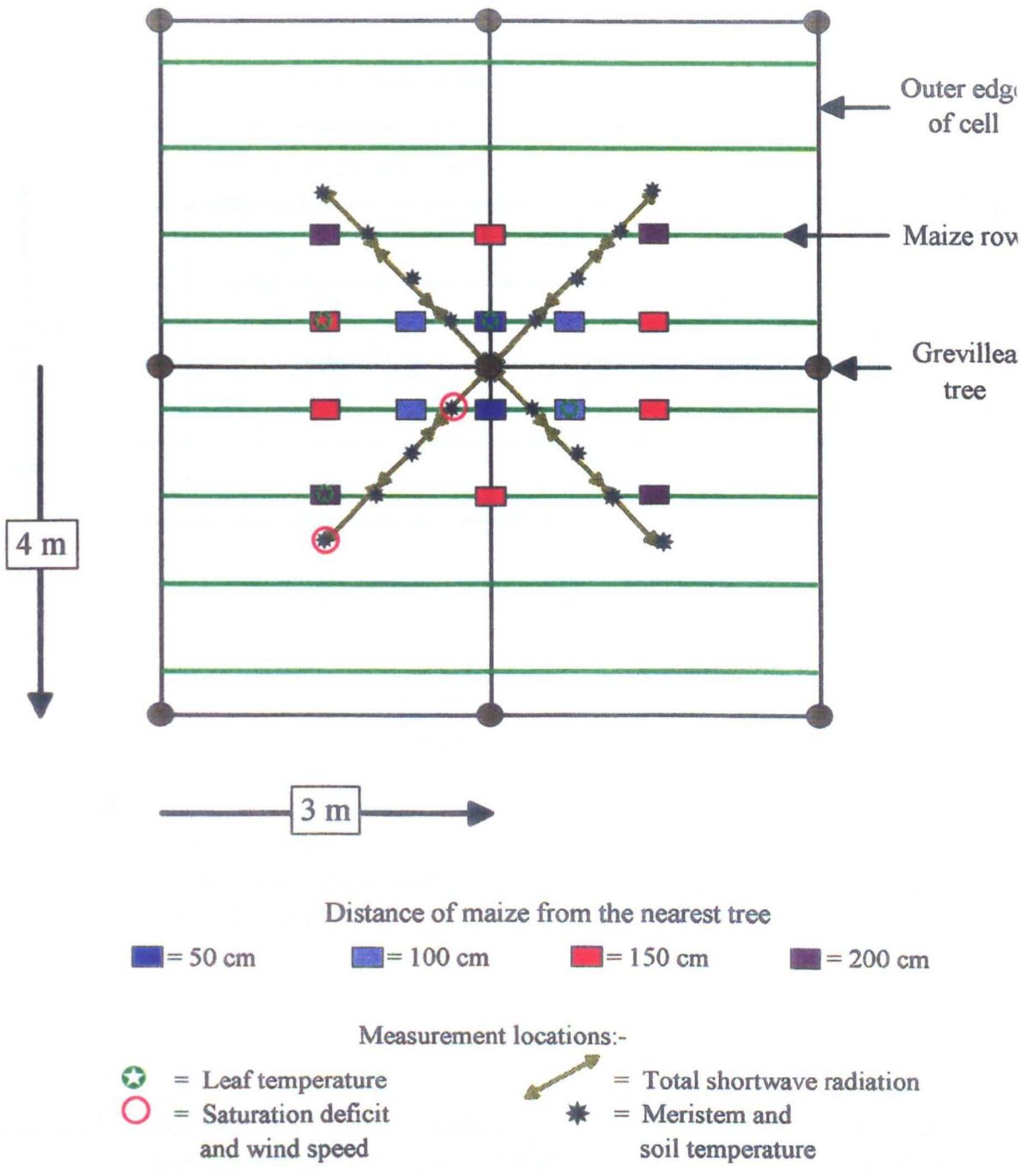


Figure 2.14 Measurement locations in the the dispersed agroforestry (CTd) plots for crop growth and development (1995 long and 1995/96 short growing seasons), saturation deficit, wind speed and leaf temperature (1995/96 short growing season) and total shortwave radiation and meristem and soil temperature (1994/95 short, 1995 long and 1995/96 short growing seasons).

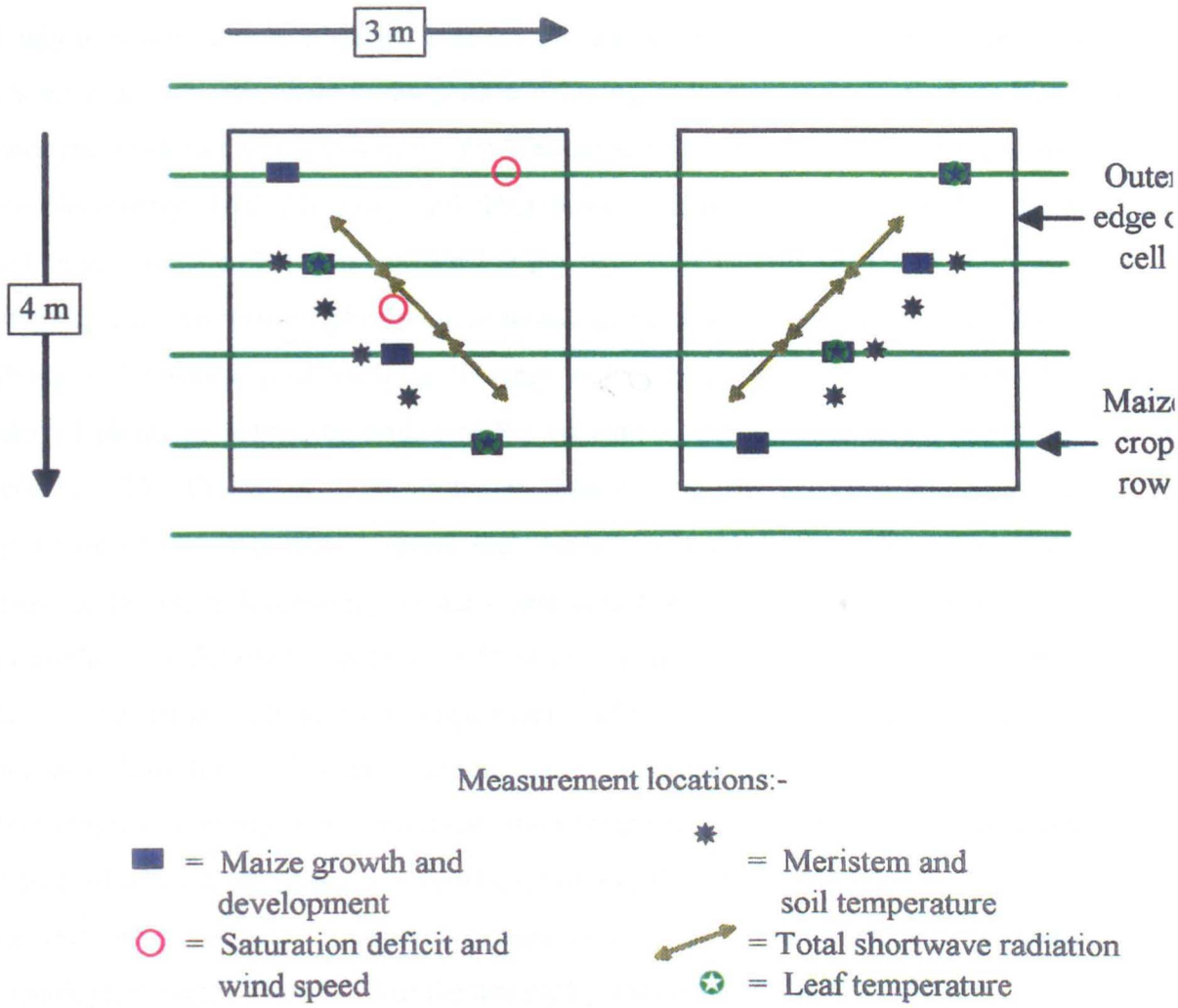


Figure 2.15 Measurement locations in the sole maize (Cg) plots for crop growth and development (1994 long to 1995/96 short growing seasons), saturation deficit, wind speed and leaf temperature (1995/96 short growing season) and total radiation (1994/95 short, 1995 long and 1995/96 short growing seasons). The locations of total shortwave radiation measurements during the 1994 long growing season were identical to those in the agroforestry plots (cf. Figure 2.10).

destructive growth analysis (NDGA) were the smallest and largest basal stem diameters to estimate the ellipsoidal cross sectional area, height to the tip of the youngest leaf, height to the top of the canopy and the number of green leaves present. Height measurements were taken from the soil surface by attaching the tape measure to a metal peg inserted next to the plant at thinning. Measurements were made three times per week in CIRUS (Monday, Wednesday and Friday) and twice weekly in the Complementary Trial (Tuesday and Thursday). Measurements followed a strict routine so that each plant was measured at the same time early in the morning of each sampling day. The critical phenological stages, germination, floral initiation, anthesis, silking and physiological maturity (Fischer and Palmer, 1984), were observed for selected plants to define the timing of the vegetative, reproductive and grain-filling periods. The timing of floral initiation was determined for each treatment by dissection of the stem and to reveal the presence of reproductive primordia. Four plants were selected randomly at daily intervals from each of the treatments until primordia were detected in at least 75 % of the plants examined on three consecutive days. Anthesis and silking were respectively defined as the point when the spikelets emerged from the leaf whorl and the silks (stigmata) appeared from the husk. Physiological maturity was determined either by the formation of a black layer at the pedicel of at least one grain per cob (Daynard and Duncan, 1969), or when 90 % of the leaf area was dry. Treatments were considered to have attained specified phenological stages when 75 % of the sampled plants reached the defined stage.

Allometric relationships for determining leaf area and above-ground biomass were established using weekly non-destructive and destructive measurements of five plants from each of the CTd and Cg plots in CIRUS or the complementary site. The plants were chosen to reflect the contrasting growing conditions and plant sizes present within these treatments. Measurements at harvest always included the parameters previously determined by non-destructive growth analyses (NDGA) before commencing destructive analyses. Total above-ground fresh weight, including leaves, stem, cobs and grain where present, was measured using a sensitive balance (resolution 0.1 g). Leaf area was determined using one of two techniques. During the first season (L94), 10 x 0.9 cm diameter disks were removed from the sampled leaves and their fresh and dry weights determined. Total leaf area was then calculated from

total leaf dry weight using the dry weight to area ratio of the disks. In subsequent seasons, leaf area was measured directly using portable or laboratory flatbed scanners (Delta-T Devices, Cambridge, U.K.). The leaves were refrigerated between harvest and completion of the leaf area measurements to prevent deterioration. The dry weight of each above-ground component was determined separately after oven-drying to constant weight at 70 °C.

Allometric relationships were established using linear regressions between allometric parameters derived from the non-destructive analyses and the destructive measurements of leaf area and above-ground dry biomass. The allometric parameters were chosen on the basis of previous work (B. McIntyre, pers. comm.) and goodness of fit; the r^2 values for the regressions established for the S94/95, L95 and S95/96 seasons ranged from 0.57 to 0.99. Leaf area and leaf dry biomass were estimated using an allometric parameter (L_{ap}) calculated from measurements of the height to the tip of the youngest leaf (h_e) and leaf number (LN) where:

$$L_{ap} = h_e^{LN} \qquad \text{Equation 2.2}$$

The remaining above-ground biomass was estimated by calculating a second allometric parameter (B_{ap}) from the product of basal stem cross-sectional area and h_e. Total above ground dry biomass was therefore calculated as the sum of the two estimates of biomass using the regression relationships established for the allometric parameters L_{ap} and B_{ap}. In addition to the 10 weekly destructive harvests, plants were sampled at various distances from trees in the CTd plots at thinning (c. 25 DAS) and on at least one other occasion in each season to test the reliability of the allometric relations established. Figures 2.16a and b illustrate the accuracy of the estimates obtained for above-ground biomass (Cg; $r^2 = 0.86$, n = 81 and CTd; $r^2 = 0.89$, n = 232) and leaf area (Cg; $r^2 = 0.85$, n = 31 and CTd; $r^2 = 0.72$, n = 61), although there does appear to be some systematic under-estimation of observed CTd leaf areas between 500 and 1000 cm^2.

The NDGA plants were harvested at maturity and the fresh weights of the leaves, stem and cobs were determined separately before oven-drying at 70 °C. The remaining

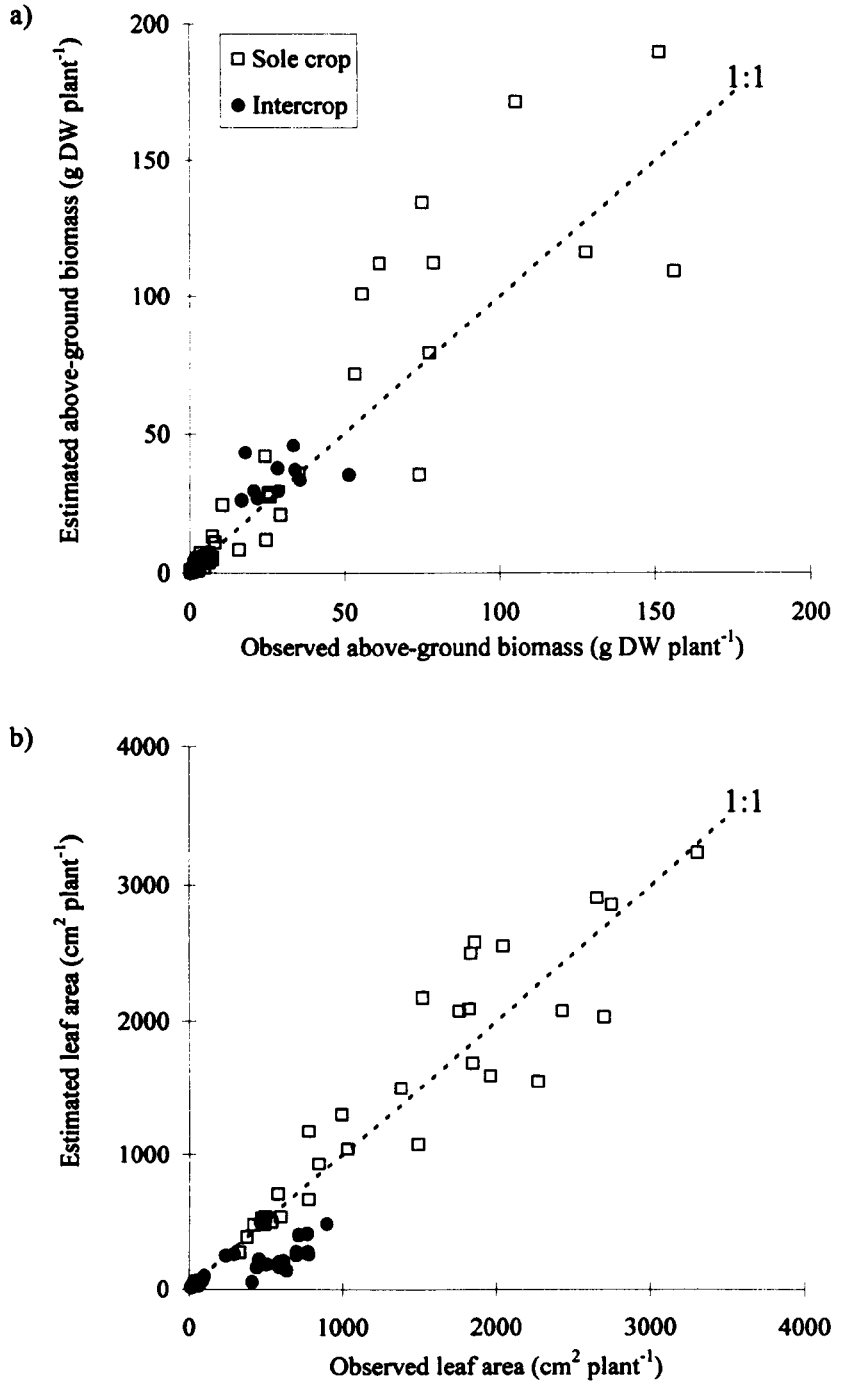


Figure 2.16 Relationship between estimated and true values for maize plants sampled from CIRUS during the 1995 long and 1995/96 short growing seasons: a) above-ground biomass of the sole crop (r^2 = 0.86) and intercrop (r^2 = 0.89) and; b) total leaf area of the sole crop (r^2 = 0.85) and intercrop (r^2 = 0.72) .

plants in the inner cells of the CTd plots and those under shade nets and in the equivalent sole plot cells (Cg 0%) were harvested on a row-wise basis and the fresh and dry weights of the bulk samples were recorded using the methods described above. Four crop rows were selected within each CTa plot and individual samples were taken from each row at 1 m intervals either side of the central tree line. The remaining plants in the sole and line planted agroforestry plots (CTc and CTa) were harvested on a row-wise basis at maturity, disregarding a 1 m guard area around each plot.

2.4.2.2 Cowpea: 1991/1992 and 1993/1994 short growing seasons

Cowpea and maize were cultivated on a rotational basis in CIRUS during for the first five seasons (S91/92-S93/94), but this rotation was replaced with continuous maize cropping during the final four seasons (L94-S95/96), due to the extensive inter-seasonal variation in rainfall making interseasonal comparisons of crop yield difficult. Maize was selected for continuous cultivation due to its importance as a staple food crop in the area and because of the disease problems that can afflict continuously cropped cowpea. Growth analysis procedures for the first five seasons are described in detail by Howard (1997), but are outlined briefly here.

Growth analysis during the first two cropping seasons was restricted to final harvest, when fresh and dry weights were recorded on a row-wise basis for the pods and haulms of cowpea (S91/92) and the stover, cobs and grain of maize (L92). The maize crop failed completely during the 1993 long rains due to poorly distributed and extremely sparse rainfall (<25 % of the seasonal average). Consequently, detailed inter-seasonal comparison of crop performance was possible only during the S92/93 and S93/94 short growing seasons and hence only for cowpea.

Cowpea was planted at four-fold greater density than maize (13333 *vs.* 3030 plants ha^{-1}), thereby permitting regular destructive harvests to be made. During the S92/93 season, all 36 plants from the top left quarter of one cell in each replicate CTd plot (Fig. 2.17) and an equivalent area of the Cg plots were harvested on six occasions at approximately 10 d intervals. Fresh weights were recorded for the leaves, stem and

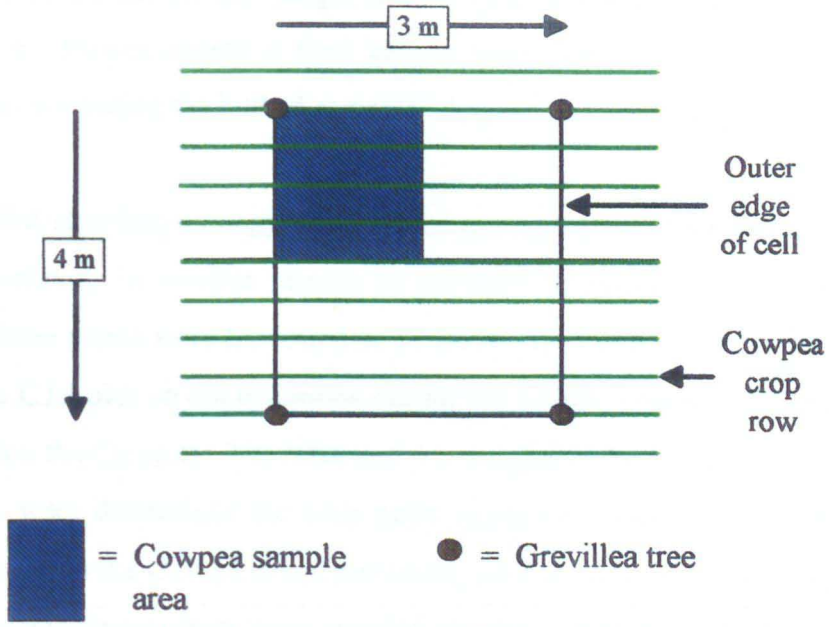


Figure 2.17 Location of the sample area for regular destructive analysis of the growth and development of cowpea in the dispersed agroforestry (CTd) treatment during the 1992/93 short growing season.

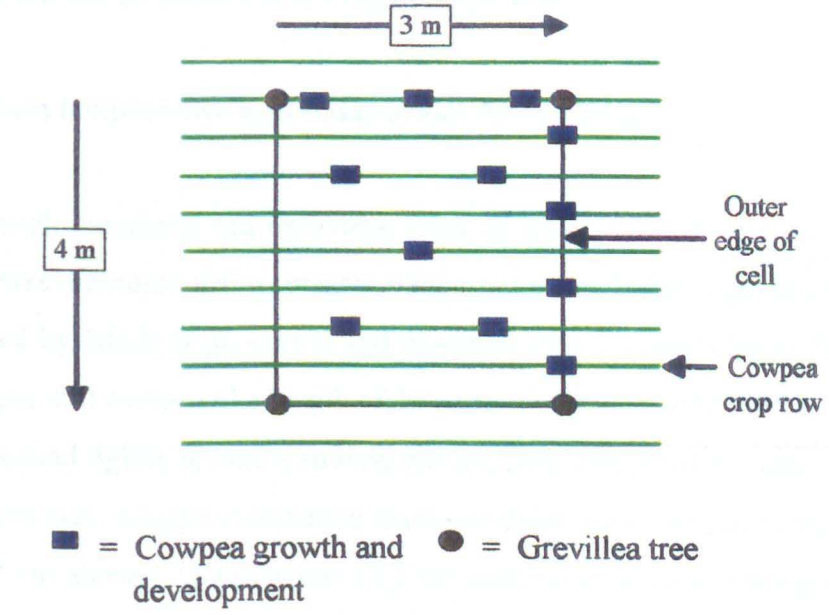


Figure 2.18 Locations of periodic growth and development measurements for cowpea in the dispersed agroforestry (CTd) plots during the 1993/94 short growing season.

pods of six plants from each plot before recombining these with the remainder of the sample to determine the total fresh and dry weights of leaves, stems and pods. Leaf area was estimated from the dry weight to area ratio of disks cut from 40 randomly selected leaves. Measurements at final harvest were made on a row-wise basis for each plot, after separating the bulked samples into pods and haulms.

A more detailed sampling strategy was adopted during the S93/94 season to examine the spatial variation in cowpea growth at different locations within cells in CTd treatment. Three plants were harvested at 12 locations within one cell (Fig. 2.18) of each replicate CTd plot on six occasions during the season; plants were sampled at 6 locations within the Cg plots. The fresh and dry weights of the leaves, stems and pods and leaf area were determined for each plant using the punched disk method. At maturity, all cells in the CTd plots not previously examined were sampled at the same locations. The remaining plants were sampled on a per cell basis in the CTd treatment and on row-wise basis in the Cg and CTc treatments. The cowpea in the CTa treatment was harvested in 1 m strips orientated parallel to the tree rows to establish the effect of distance from the trees on crop yield.

2.5 SAP FLOW MEASUREMENTS ON TREES AND CROPS

2.5.1 Constant temperature heat balance sap flow technique

Sap flow through the stems and excavated roots of grevillea trees and the stems of maize plants was measured using constant temperature heat balance gauges similar to those described by Ishida *et al.* (1991) and modified by Khan and Ong (1995) (Plate 2.7). The heater coil comprised a length of 36 gauge constantan wire with a resistance of 15 ohms, wound tightly around a smooth and uniform section of the stem or root to ensure good contact. Copper-constantan thermocouples were secured to the stem or root surface 2 cm above (T_d) and below (T_u) the heater coil using insulating tape; the thermocouple lead wires were wrapped once around the stem or root for support and to minimise conduction down the wires. Thermocouples were also attached to the heater coil (T_h) and the stem or root 4 cm upstream of the heater (T_o); the latter served as a reference for controlling the heater input. The installation was insulated with a

Plate 2.7 (top left and top right) Heat balance gauges being fitted to grevillea roots: the gauges were insulated with styrofoam jackets and silver foil and covered by black polythene tents to avoid errors introduced by thermal energy exchange; (bottom left) heat balance gauges installed on grevillea trunks as far from the ground as possible to avoid thermally-induced errors; and (bottom right) heat balance gauge on maize.

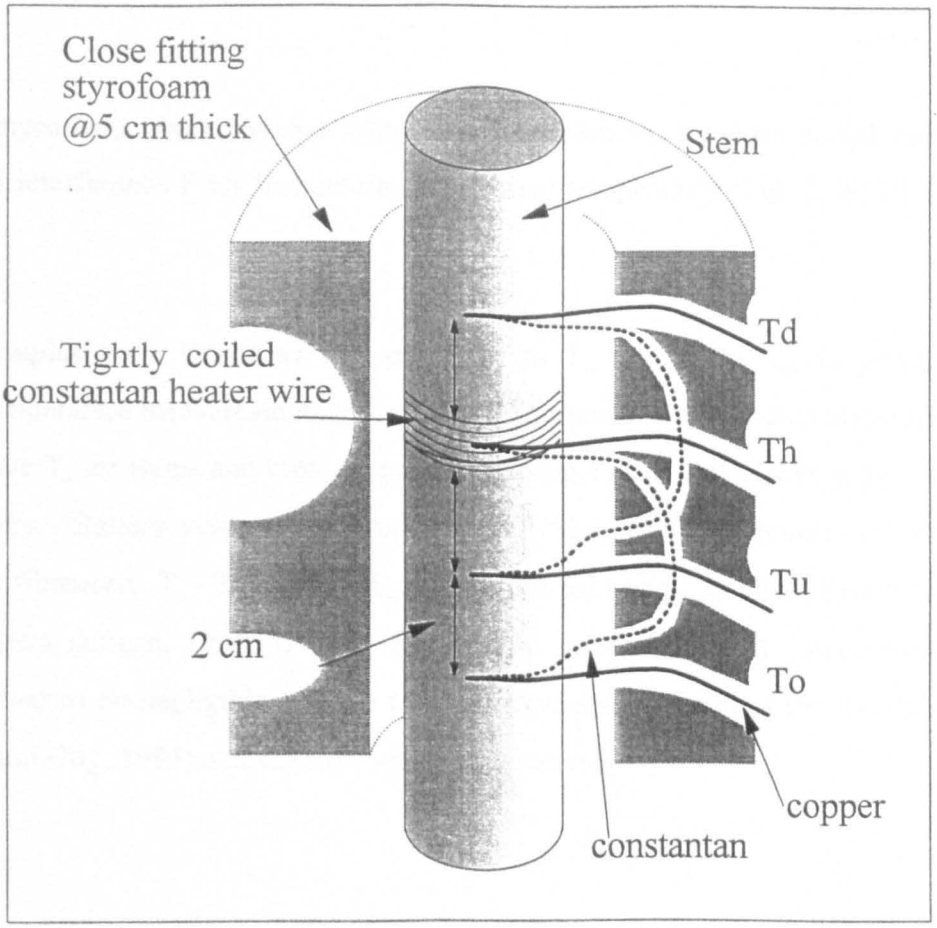


Figure 2.19 Illustration of the constant temperature heat balance apparatus (taken from Howard 1997). Temperature measurements were taken at the heater (Th) and 2 (Tu) or 4 (To) cm upstream of the heater and 2 cm downstream (Td) of the heater. See text for explanation.

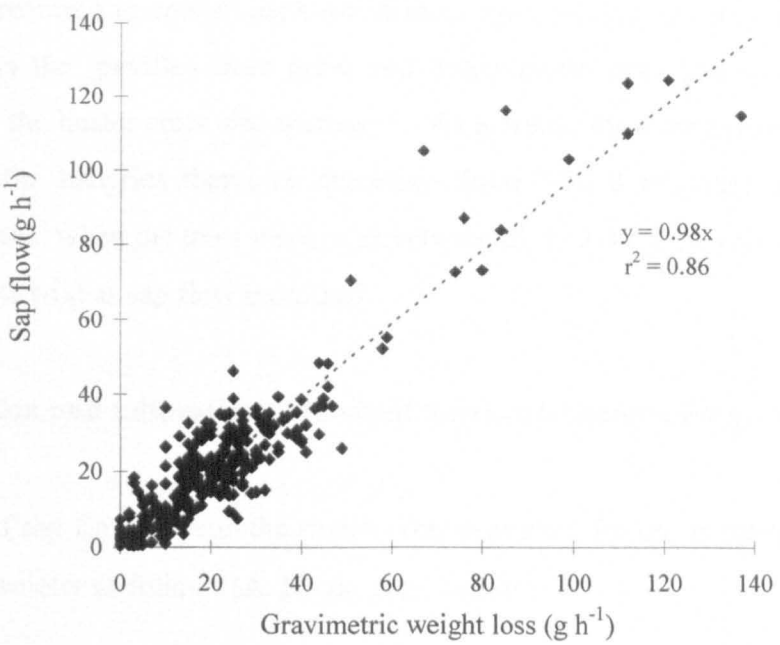


Figure 2.20 Calibration of the heat balance sap flow gauges for maize by comparison of sap flow with gravimetric weight loss for 8 potted maize plants.

close-fitting styrofoam block covered with aluminium foil to minimise radial heat exchange and interference from fluctuations in ambient temperature (Fig. 2.19; Plate 2.7).

The thermocouples were linked as two pairs, T_h to T_o and T_u to T_d, to permit differential temperature measurements to be made. Thermocouple T_h was maintained 5 or 8 °C above T_o for stems and roots respectively using a relay and power provided by a car battery. Battery voltage, the count time of the relay (loop count) and the temperature differences, T_h - T_o and T_d - T_u, were recorded using Campbell Scientific 21X Dataloggers (Logan, Utah, USA). Radial and conductive heat losses were initially assumed to be negligible relative to convective transfer during the daylight hours (Khan and Ong, 1995) and sap flow was estimated as:

$$J_m = \frac{V^2}{R \times C_w (T_d - T_u)} \qquad \text{Equation 2.3}$$

where J_m represents sap flow (g h^{-1}), V and R denote the voltage (V) and resistance (ohms) of the heater wire, and C_w is the specific heat of water (4.18 J g^{-1} $°C^{-1}$). One datalogger was required to control each set of three heat balance systems and record their output. As the grevillea trees grew and transpiration rates increased, power consumption by the heater coils also increased. As a result, the time period between replacement of the batteries therefore decreased from 7-10 d intervals during the 1992/93 short rains, when the trees were relatively small, to 2-4 d intervals during the latter stages of the trial as sap flow increased.

2.5.2 Adaptation and calibration of the heat balance technique for grevillea.

Measurements of sap flow through the trunks were corrected for errors resulting from differences in diameter as follows (A. Khan, pers. comm.):

$$J_n = \frac{J_m}{(0.0001d^2) - (0.0031d) + 1.0552} \qquad \text{Equation 2.4}$$

where J_n denotes the corrected sap flow (g h^{-1}) and d is the diameter of the trunk (mm). As this calibration was limited to stems with a maximum diameter of c. 9 cm, the heat balance gauges were installed immediately below the canopy, so that trunk diameter remained within the calibration range throughout the trial. This approach had the additional benefit of avoiding thermal interference from the soil, a problem recognised by Khan and Ong (1995) as having a potentially serious influence on the reliability of heat balance measurements. The risk of thermal interference resulting from uneven solar heating of the trunk was minimised by covering the stem with reflective foil.

Restrictions on the availability of dataloggers limited the scope, frequency and replication of heat balance measurements to some extent. Six heat balance gauges were generally available, three of which were fitted to Td trees and three to CTd trees. Heat balance gauges were left attached to the rapidly growing trees for a maximum of two weeks to avoid girdling of the bark by the heater coil as stem diameter increased.

2.5.3 Adaptation and calibration of the heat balance technique for maize.

As maize differs physiologically and morphologically from grevillea, a separate calibration was required. Maize plants were grown individually in 20 l plastic containers filled with soil. At about 45 days after sowing (DAS), eight plants were selected for the calibration and the soil surface of each container was covered with polythene to prevent evaporation and ensure that transpiration was the only source of water loss. The plants were transferred to a polythene shelter to provide protection against wind and facilitate accurate gravimetric measurements of transpiration using a load cell. The oldest two or three leaves were removed to allow heat balance gauges to be attached to smooth and circular sections of the stem; this process was also carried out during field measurements. Removal of these older and senescent leaves had little effect on sap flow since their contribution to total transpiration was small. The gauges were left attached for three days and each plant was placed in turn on a load cell for one full day to obtain direct gravimetric measurements of transpiration for comparison with the output from the heat balance gauges. A close correlation ($r^2 = 0.86$, $n = 295$) was obtained between the gravimetric and heat balance estimates of transpiration (Fig. 2.20). The equation for the linear regression (Eq. 2.5) was used to obtain corrected

sap flow measurements (J_z) for maize from the initial uncorrected heat balance values (J_m):

$$J_z = 0.9771 (J_m) \qquad \text{Equation 2.5}$$

The frequency and continuity of measurements for maize were limited by the age and physical size of the plants and the need to use the same equipment for the trees. Sap flow gauges could not be used for maize until the plants had produced at least five leaves and/or a stem diameter greater than 18 mm; thus the heat balance approach could not be employed until approximately one third of the season had been completed. The use of this sap flow technique on maize was highly labour intensive since the gauges could not be left attached for longer than three days because the heater coil could constrain stem growth and cause injury. Priority was therefore given to the trees, for which the heat balance approach was better suited, and an alternative method was adopted for maize in which a PP Systems CIRAS 1 InfraRed Gas Analyser (IRGA) was used for intensive measurements of transpiration (cf. Section 2.6).

2.5.4 Calibration of the heat balance technique for roots.

Since the heat balance technique was originally calibrated for use on stems, a separate calibration was carried out to validate the heat balance method for roots (Lott *et al.*, 1996). In order to achieve this, lateral roots were carefully excavated, leaving a section still enclosed within an intact block of soil. The exposed root was severed just beyond the soil block, leaving the rest of the root connected to the tree. The soil blocks were placed in 10 l plastic basins and kept well-watered and fertilised to encourage root development and water uptake. The soil surface was covered with styrofoam and aluminium foil to minimise evaporative water loss and heating by solar radiation (Plate 2.8). After four weeks, a section of root closer to the trunk was exposed and a sap flow gauge attached; the installation and any part of the root still exposed were covered with expanded polystyrene and aluminium foil. The entire installation was covered with a "tent" made from a double layer of opaque polythene with a 2 cm wide air gap between the layers to minimise the thermal errors introduced

Plate 2.8 Calibration of heat balance gauge for grevillea roots. Excavated roots enclosed within undisturbed blocks of soil and still attached to their parent trees were placed on load cells to measure absorption gravimetrically. The terminal portion of the root was severed.

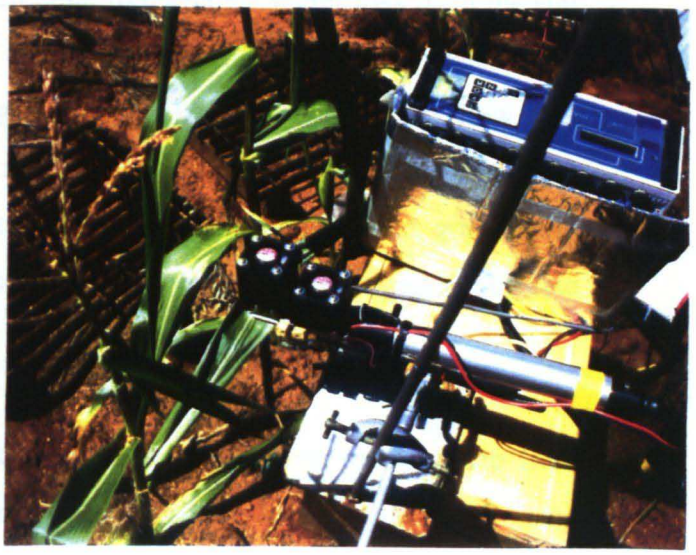


Plate 2.9 PP Systems CIRAS 1 IRGA and Parkinson cuvette. The reflective insulation covering the rear of the IRGA avoided condensation forming in the air supply filter columns.

Plate 2.10 Placement of solarimeters in the Td (above) and Cg (right) treatments. Note the groups of three solarimeters aligned in different orientations around individual trees and the sharply defined shadow pattern cast by the tree canopy (above), and the placement of solarimeters to sample adjacent crop rows (right).

by differential heating of the soil due to irregular tree shade. Water loss from the soil block within the basin resulting from absorption by the roots was determined gravimetrically at 1 min intervals using a top pan balance, whilst sap flow was measured at 3 s intervals and recorded as 15 min means. Because there were no branch roots between the basin and the heat balance installation, the gravimetric measurements permitted the heat balance system to be calibrated against absolute measurements of water uptake.

Previous experience has shown that heat balance gauges used to measure sap flow through stems should be located as far as possible from the soil surface to minimise errors induced by conductive or convective transfer of heat to the thermocouples (Khan and Ong, 1995). As this is clearly impossible with roots, the effects of ambient temperature changes must be quantified and corrected for, particularly those arising from differential heating of the soil caused by diurnal variation in shading by the tree canopy. To achieve this, a freshly excised and therefore non-conducting length of root of similar diameter was placed alongside each live root under examination and heat balance systems were installed at the same relative positions on the living and excised roots, in a modification of a technique previously recommended for stems (Baker and van Bavel, 1987). The measured sap flow values (J_m) for live roots were corrected as follows:

$$J_s = \frac{J_m(D_L)}{(D_L - D_C)} \qquad \text{Equation 2.6}$$

where J_s represents the measured sap flow (g h^{-1}) corrected for errors introduced by external heat sources, and D_L and D_C are respectively the temperature differentials (T_u - T_d) for the live and excised roots.

Conduction of heat from the heater in the axial and radial directions and storage of heat within the root may also cause overestimation of sap flow (Fichtner and Schultze, 1990). To correct for this, power absorption by the non-conducting excised root was determined from the loop count and battery voltage and the following correction applied:

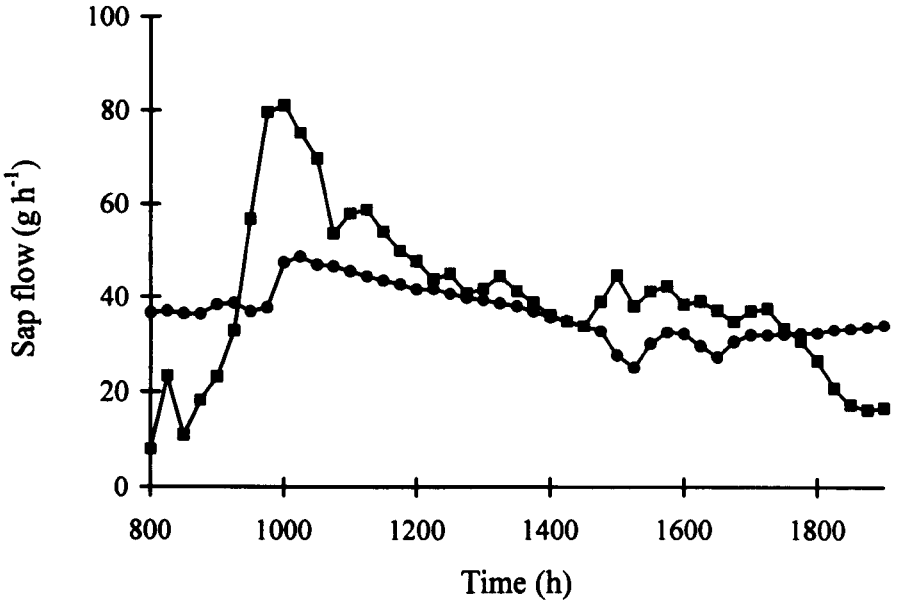


Figure 2.21 Uncorrected sap flow values for an intact living root (squares) and an adjacent freshly excised non-conducting root (circles).

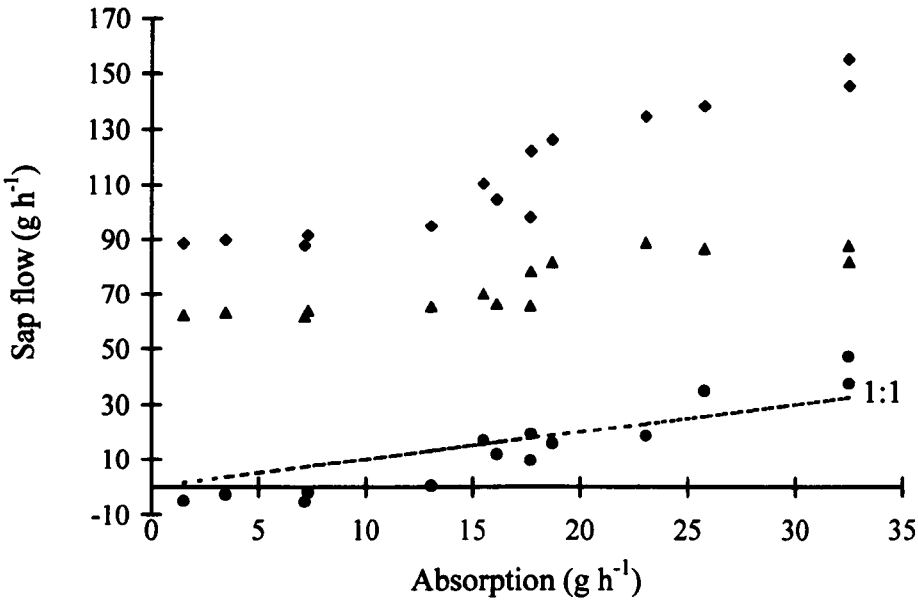


Figure 2.22 Relationship between sap flow estimated using the heat balance method and absorption determined gravimetrically (1:1 line). Heat balance values: uncorrected (diamonds); corrected for external heat sources (triangles); and corrected for external sources and internal losses of heat (circles). Data obtained using roots from two trees.

$$J_x = J_s - \frac{0.01913 \times (1.4\,C_c - 10) \times V_c^2}{(D_L - D_C)}$$ Equation 2.7

where J_x is the measured sap flow (g h^{-1}) corrected for both sources and losses of heat, and C_c and V_c are respectively the loop count and heater voltage for the excised root. A similar method was adopted by Khan and Ong (1995) to correct for over-estimation of sap flow through the trunks of large trees.

Figure 2.21 clearly demonstrates that the reliability of uncorrected heat balance measurements of sap flow through roots may be seriously compromised by thermally induced errors since an apparent sap flow was detected in excised roots placed beside living roots; for much of the day the values recorded for living roots were little greater than those for the excised roots. Because the latter were non-conducting, the apparent sap flow is clearly an artefact. The temperature differentials recorded for the excised roots may be used to correct for errors in the sap flow values for living roots caused by external sources of heat using Equation 2.6. Figure 2.22 shows that the uncorrected sap flow values for living roots obtained using heat balance gauges (diamonds) were substantially greater than the corresponding gravimetric values. Correction for errors resulting from external heat sources reduced the difference between the heat balance and gravimetric estimates, but a substantial discrepancy is still apparent (Fig. 2.22, triangles). Additional correction for conductive heat losses and storage of heat within the root using Equation 2.7 produced a further improvement in fit between the heat balance and gravimetric values (Fig. 2.22, circles), as reported previously for stems by Ishida *et al.* (1991) and Khan and Ong (1995). A close fit to the 1:1 line was obtained at flow rates above 15 g h^{-1} ($r^2 = 0.86$), but at lower flow rates the heat balance values underestimated the true sap flow, even after correction for thermal errors. Similar underestimates of low flow rates have been reported for the stems of other species (Baker and van Bavel, 1987; Sakuratani, 1990; Groot and King, 1992; Senock and Ham, 1993).

2.6 PHOTOSYNTHESIS AND TRANSPIRATION BY CROPS

Many of the approaches adopted in CIRUS relied on techniques such as the heat balance method (Section 2.5) which provide medium to long-term estimates of resource capture and conversion efficiency, but cannot readily be used to investigate spatial variation within the system (e.g. different layers within the canopy or locations relative to the trees). Consequently, these longer term techniques cannot provide a mechanistic understanding of the responses to shading of understorey crops. Such information can most effectively be provided using a portable infrared gas analysis system (IRGA) capable of rapid field measurements of photosynthetic and transpiration rates per unit area of individual leaves, and using the data obtained to construct light response curves to assess the impact of shade. A PP Systems CIRAS 1 IRGA (Hitchin, Herts, U.K.) provided by the Royal Society permitted the longer-term information on resource capture and use obtained from CIRUS to be significantly extended by allowing the dynamics of tree/crop interactions to be examined in terms of:

- variation in net photosynthesis (P_n), transpiration (Et) and the conversion coefficients for light and water at various locations around trees;

- interactions between above and below-ground competition for light and water.

2.6.1 PP Systems CIRAS 1: operation and use in field conditions

The CIRAS 1 employs the open or steady-state approach to photosynthesis measurements (Sestak *et al.*, 1971; Pearcy *et al.*, 1989), which involves passing a continuous stream of air of known CO_2 and H_2O concentration through a chamber containing a known area of intact leaf. Photosynthesis and transpiration by the enclosed leaf tissue depletes the air passing through the chamber of CO_2 and enriches it in water vapour relative to the air entering the chamber. The net rate of photosynthesis (P_n) may be calculated from the difference in CO_2 concentration (C) and the flow rates (U) of air entering and leaving the chamber as follows:

$$P_n = \frac{U_e C_e - U_o C_o}{L} \qquad \text{Equation 2.8}$$

where the subscripts e and o denote the air entering and leaving the chamber and L represents the enclosed area of the leaf.

Certain modifications to the CIRAS 1 were necessary to allow accurate measurements to be made in CIRUS. The air immediately adjacent to the air intake of CIRAS 1 was subject to variations in H_2O and CO_2 concentration resulting from the perspiration and breath of the operator, the frequent strong breezes at the experimental site, and the rapid photosynthesis, respiration and transpiration of the tree and crop canopies. The resulting instability in the composition of the air stream entering the leaf chamber adversely affected the measurements of photosynthesis and transpiration. To overcome this problem, an 18 m length of rubber tubing was severed part way along its length and a 2 l plastic vessel was inserted to create a mixing volume; one end of this airline was attached to the CIRAS 1 inlet and the other was suspended above the tree canopy using a 10 m long pole. A further problem was that the high radiation levels in Machakos were capable of heating the clear perspex absorber columns mounted on the rear of CIRAS 1, causing condensation to form and thereby affecting the humidity of air drawn into the leaf chamber during analysis. Consequently, the reliability of the transpiration measurements could be compromised. A simple silver foil reflective screen was therefore placed over the absorber columns to minimise radiative heating (Plate 2.9).

2.6.2 Routine measurements of crops

The IRGA was available from the 1994/95 short growing season onwards and was used intensively during the 1995 long and 1995/96 short growing seasons. Measurements were routinely made either four times per day at 2 h intervals commencing at 1000 h local time, or alternatively once around midday using an artificial light source to construct photosynthetic light response curves for the crops in each of the treatments examined. To allow successive measurements to be made

using the same area of leaf, a fine permanent marker was used to trace the outline of the leaf chamber on the leaf surface after the first measurement. Non-destructive growth analyses were carried out two or three times per week for all plants used for IRGA measurements to determine their biomass and leaf area.

2.6.3 Light response curves

The photosynthetic responses of maize and cowpea to varying fluxes of photosynthetically active radiation (PAR) were determined using an artificial light source powered by a 12 v car battery. The light source was attached to the leaf chamber, which was supported at the leaf level using a clamp stand (Plate 2.9). The PAR flux was progressively reduced by placing a series of eleven neutral filters between the light source and the leaf chamber. The leaf was allowed to equilibrate to each PAR level before measurements were recorded and the entire photosynthetic response curve required c. 20 minutes to complete.

2.7 EFFECTS OF NATURAL AND ARTIFICIAL SHADE ON THE CROP MICRO-ENVIRONMENT

Shading by the tree canopy or shade netting alters the microclimate experienced by understorey crops in a highly complex manner. Thus, the extent of the microclimatic changes induced varies spatially depending on proximity to the nearest tree and the planting arrangement and density of the trees, and also temporally in response to diurnal fluctuations in solar angle and climatic conditions and longer term changes in shading intensity as the trees mature. To characterise these effects, microclimatic conditions were monitored routinely, but with greater frequency during the period between the L94 and S95/96 seasons.

2.7.1 Radiation

Total short-wave radiation incident upon or transmitted by sole and intercropped grevillea and maize was measured using unscreened tube solarimeters (Delta-T Devices, Cambridge, UK) with an effective area of length 85 cm. These are based on

a linear thermopile detector painted with a black and white checker-board pattern; when exposed to radiation, this pattern results in differential heating of the black and white junctions, producing a voltage output which is directly proportional to the number of junctions involved and the temperature difference generated by the incident radiation. These instruments measure direct and diffuse solar radiation within the visible and infra-red wavelengths (350-2500 nm), but are insensitive to wavelengths longer than 3000 nm due to the screening effect of their Pyrex enclosures. The solarimeters were mounted horizontally and in parallel, at fixed heights of 100 cm (half the mean expected canopy height of sole maize) or at ground level using adjustable stands (Plates 2.10a and b). Following the procedures advised by Monteith (1993), the instruments were calibrated prior to each growing season (twice annually) against four standard solarimeters. The tubes were cleaned and checked for condensation on a daily basis. To avoid condensation within the instruments, which may be a serious problem during rainy periods, perforated packets of Dryrite crystals were placed in each tube. If condensation formed, the solarimeters were removed from the field, unsealed and placed in an oven at 60 °C for 24 h to remove the moisture and regenerate the Dryrite crystals. Once the seals had been replaced and the tubes had cooled, they were returned for re-calibration and further to their original position within the trial.

Radiation interception by vegetation may be determined from solarimeter measurements of irradiance above and below the canopy (Monteith *et al.*, 1981). In the case of agroforestry (or other mixed cropping systems), the instruments must be appropriately positioned to measure radiation levels above and below both the tree and crop canopy. Solarimeters were therefore placed at defined positions immediately above ground level in the sole maize (Cg; 6 tubes in plots 12 and 13; Plate 2.10b) and dispersed agroforestry treatments (CTd; 12 or 16 tubes in plot 5), and at a height of 100 cm in the sole grevillea treatment (Td; 12 or 16 tubes in plot 4; Plate 2.10a) and on open land outside CIRUS (4 tubes). The placement of solarimeters was designed to provide optimal sampling of the variation created by row spacing and the non-uniform canopy cover provided by the trees. This was achieved by combining solarimeters in groups of four (L94) or three (S94/95, L95 and S95/96) to span two crop rows (2 m) in the Td and CTd plots. The solarimeters were arranged in arrays

radiating from individual trees to sample the radiation environment at 90° intervals around the tree (Figs. 2.13 and 2.14) and this orientation was mirrored in the Cg plots (Fig. 2.15). Their output was recorded as hourly means using Campbell 21X dataloggers (Campbell Scientific, Logan, Utah). The four solarimeters located on open land were used as references to record incident radiation and the values obtained were routinely validated against the Kipp solarimeter located at the CIRUS meteorological station. Intercepted radiation was calculated as the difference between incident radiation and the transmitted values for each sampling location.

2.7.2 Meristem and soil temperatures

Soil and meristem temperatures were measured using copper/constantan thermocouples (24 gauge wire, Omega Engineering Inc. #PR-T-24) connected to a Campbell 21X datalogger. The thermocouple junctions were coated with high thermal conductivity epoxy resin (heat sink bonder; RS Components #850-984) to prevent water penetration. Thermally-induced errors were minimised by wrapping the thermocouple lead wires in reflective foil and supporting them above the soil on ropes; the thermocouples used to measure meristem temperature were protected from direct sunlight by attaching them to the up-slope side of the plant.

Spatial variation in temperature was quantified by placing thermocouples (Figs. 2.13, 2.14 and 2.15) at the same locations as plants used for non-destructive growth analysis and tube solarimeters; this approach enabled the impact of tree shade on the radiation and thermal micro-environments to be related directly to the responses of the understorey crops. Four thermocouples were located parallel to each solarimeter, two of which were used to measure soil temperature at a depth of 2 cm between the crop rows and two to determine meristem temperature in maize. Similar measurements were made in the Cg 0%, Cg 25% and Cg 50% treatments (plots 12 and 13) and in plots 7 and 8 of the Complementary Trial (S94/95 and L95 only) using the arrangement described for the CTd treatment. Each thermocouple position was replicated four times and their output was recorded individually.

Meristem temperature was estimated between c. 0-45 DAS by placing thermocouples in the soil adjacent to plants at a depth of 2 cm since the meristem of maize remains beneath the soil surface until internode elongation commences during the reproductive phase (Norman *et al.*, 1984). After c. 45 DAS, meristem temperature was estimated by inserting the thermocouple into the leaf sheaths or stem.

In a short review of the various systems used to predict tropical maize phenology under field conditions using thermal time, Lenga and Keating (1990) pointed out how little information existed on the relative merits of each system. In particular, they highlighted the large disagreement between base and optimum temperatures established under controlled environment experiments, where much of the work has been carried out, and those determined from field experiments. Values reported for base (Tb) and optimum (To) temperatures range from 0-10 and 26-34 °C respectively, with the values for Tb generally being lower under field conditions than in controlled environment studies. Squire (1990) however, suggests that the large variation in the development rates of tropical crops in the field is not attributable to differences in their cardinal temperatures but rather variation in thermal duration. Lenga and Keating (1990) also pointed out that many studies of the impact of thermal time on development have depended on measurements of mean daily air temperature, which has two fundamental consequences. Firstly, air temperature provides a poor approximation of meristem temperature in cereals, particularly during the early stages of growth when the meristem is still located below ground. Consequently, soil temperature or plant temperature measured close to the meristem are more appropriate variables (Walker, 1970; Coeloho and Dale, 1980; Ong, 1983). Secondly, mean daily temperatures hide the diurnal fluctuations that are so influential in determining developmental rates. For example, a constant temperature of 10 °C might preclude development (assuming a Tb of 10 °C) whereas a diurnal range of between 6 and 14 °C (mean of 10 °C) would allow development to proceed. To illustrate this, Khalifa and Ong (1990) subjected seeds of pearl millet to supra-optimal temperatures by exposing them for short periods (2-4 h) to temperatures of 40-45 °C. These short periods of supra-optimal temperatures reduced germination rate by 25-100 % relative to the control (constant temperature of 30 °C). Consequently, it may be concluded that calculations of thermal time for field grown tropical crops should utilise

frequently recorded temperature measurements that approximate closely to the plant meristem temperature.

Thermal time (θ), measured in units of degree days (°Cd), was calculated according to equations adapted from Garcia-Huidobro *et al.* (1982) using the recorded mean hourly values for meristem temperatures (T):

$$\theta_1 = \frac{(T - T_b)}{24} \qquad \text{for } T_b <= T <= T_o \qquad \text{Equation 2.9}$$

$$\theta_2 = \frac{(T_m - T) \times R}{24} \qquad \text{for } T_o < T <= T_m \qquad \text{Equation 2.10}$$

where T_b is the base temperature below which development ceases, T_o is the optimum temperature for development, T_m is the maximum temperature above which development ceases and R is a ratio used to convert thermal time accumulated below T_m into degree-days above T_o and is equivalent to:

$$R = \frac{(T_o - T_b)}{(T_m - T_o)} \qquad \text{Equation 2.11}$$

By summing the calculated values for θ_1 and θ_2 over specific periods, from emergence to anthesis for example, the thermal durations for developmental stages can be ascertained. In this study, T_b, T_o and T_m were assigned values of 8, 32, 45 respectively, after an extensive literature survey with particular reference to the work of Cooper (1979), Fischer and Palmer (1984) and Lenga and Keating (1990).

2.7.3 Weather and additional microclimate measurements

An automatic weather station was located at the CIRUS site throughout the experiment. Initially the weather station was located outside the site (October 1992 - February 1994), but thereafter the instruments were mounted on a height-adjustable mast to maintain them above the tree canopy between plots 10 and 11. The variables

measured were wet and dry bulb temperatures (using an Institute of Hydrology type aspirated psychrometer), wind speed and direction (Campbell Scientific, Leics, U.K.), and incident radiation (Model CM5, Kipp and Zollen, The Netherlands). All variables were measured at 1 minute intervals and hourly mean values were stored using a data logger (Campbell 21X, Campbell Scientific Instruments, U.S.A.). Rainfall was measured using a tipping bucket rain gauge positioned approximately 20 m uphill of the nearest trees.

Institute of Hydrology personnel collected additional microclimatic measurements to the radiation and temperature measurements described above (Section 2.7.1 and 2.7.2). These included measurements of wet and dry bulb temperatures (IH type aspirated psychrometer) and wind speed and direction (Campbell Scientific, Leics, U.K.) made using instruments positioned next to a tree in Plot 10 at ¾ tree height and ¾ crop height and also at ¾ crop height in the middle of an individual cell.

2.7.4 Soil moisture

Soil moisture measurements conducted by Institute of Hydrology staff between May 1993-July 1997 are reported in detail by Wallace *et al.* (1995), Jackson and Wallace (1997) and Jackson *et al.* (1997). The techniques and sampling locations involved are outlined briefly here to demonstrate the compatibility of the above and below-ground datasets for the purposes of data analysis and simulation modelling.

Volumetric soil water content was measured at weekly intervals using a 'Wallingford' neutron probe (Bell, 1987) and 75 access tubes installed to a depth of at least 10 cm into the bedrock. Due to the extensive variation in soil depth across the site (cf. Fig. 2.4), the access tubes ranged in depth from 40-180 cm. Tubes were installed in three of the four replicates of the Cg, CTd, Td and CTc treatments at the positions shown by Wallace *et al.* (1995, Fig. 5). The measurement locations in the CTd and Td treatments permitted the influence of proximity to the nearest tree on the soil water content profiles to be examined within one quarter of the cell enclosed by four adjacent trees. The results were then scaled up to provide information on the spatial

variation in soil moisture content within the entire cell, in a manner analogous to the crop growth analysis and micro-meteorological datasets.

Time Domain Reflectometry (TDR) was used to measure soil water content at hourly intervals at depths of 5, 15, 25 and 35 cm in one replicate of the Cg, CTd and Td treatments (plots 12, 10 and 11 respectively) at the locations indicated by Wallace *et al.* (1995, Fig. 5). The data obtained provided accurate measurements of soil moisture content within the surface horizons with a high temporal and spatial resolution.

Soil evaporation was measured using 24 micro-lysimeters installed in plots 2, 10, 11 and 12 (bare soil, CTd, Td and Cg treatments). These were grouped in sets of four, two within and two between crop rows, and arranged on a north, south, east and west orientation around a single tree in the CTd and Td treatments (Wallace *et al.*, 1995). The lysimeters were weighed twice daily at 0800 and 1800 h for 10-12 days following rainfall during the growing seasons. Some lysimeters were also placed on load cells to record hourly rates of evaporation.

50 m^2 runoff plots were installed in three of the four replicate plots in the Cg, Td, CTd and CTc treatments in September 1993 (Fig. 3.2; Plate 3.1; Wallace *et al.*, 1995, Fig. 3). These channelled water into 1 m^3 collection tanks, enabling the volume of runoff and the quantity of soil eroded to be determined for specific rainfall events.

Redistribution of rainfall by the tree canopy was quantified in terms of throughfall and stemflow from November 1994 onwards. Throughfall was measured in plots 10 and 11 (CTd and Td) using twelve rain gauges set out in an identical arrangement to the TDR sensors. Two rain gauges were placed at random in Cg plot 12. Stemflow gauges fitted to nine trees in each of the CTd and Td treatments (plots 10 and 11) were used to measure the proportion of intercepted rainfall channelled down the trunk.

2.8 STATISTICAL ANALYSIS, AND DATABASE MANIPULATION AND MANAGEMENT

Means and standard errors were calculated, and analysis of variance, t-tests and regression analysis were carried out using Excel, Genstat and Statistica software

packages. The extensive database collected during the field campaign was collated using the Q&E database package and manipulated in Excel spreadsheets.

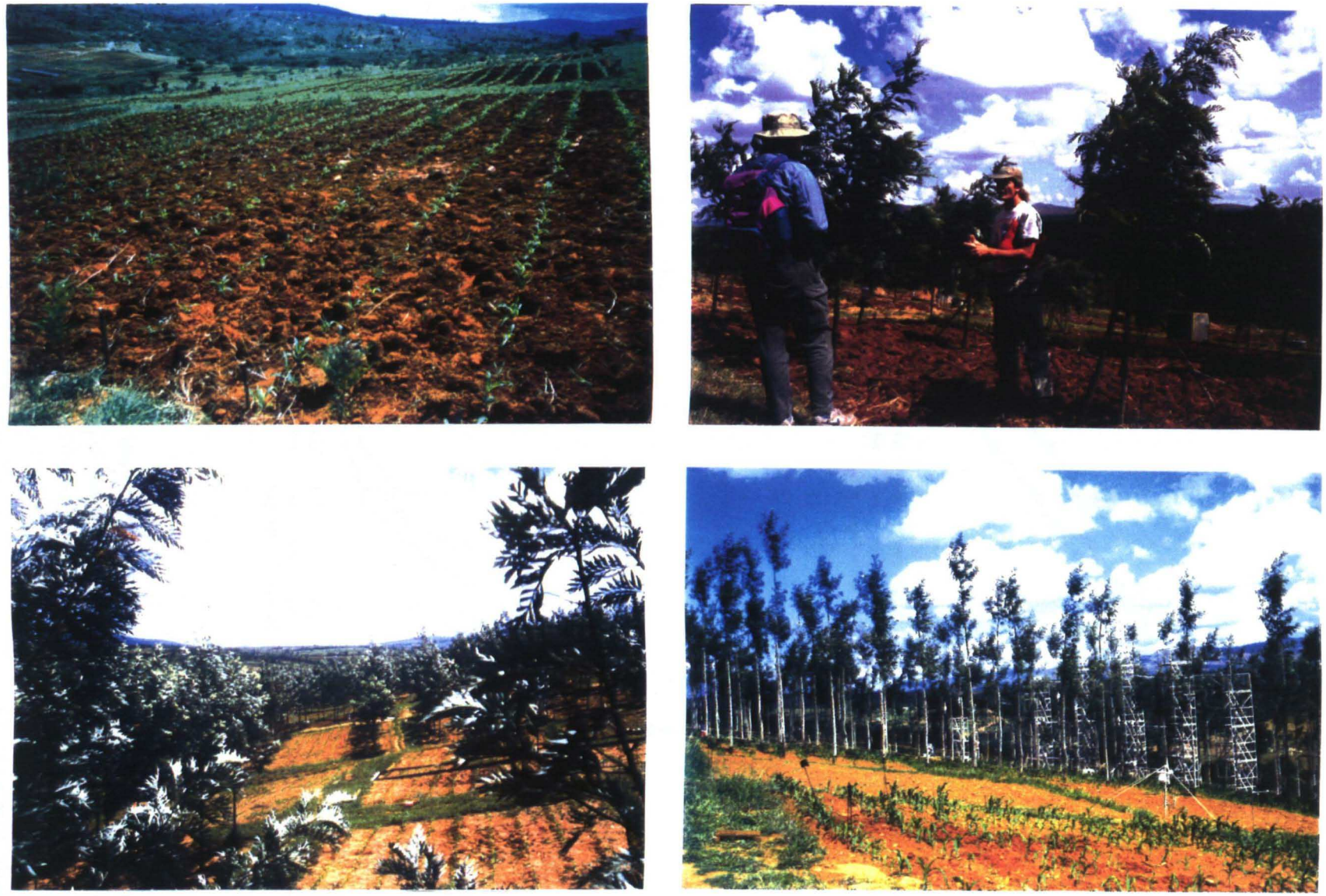


Plate 3.1 Growth of grevillea: the trees were 0.3 m tall by January 1992 (top left, foreground), c. 3 m tall by March 1993 (top right), c. 7 m tall by March 1996 (bottom left) and c. 8.5 m tall by March 1997 (bottom right); the access towers used by IH staff to sample the canopy are visible.

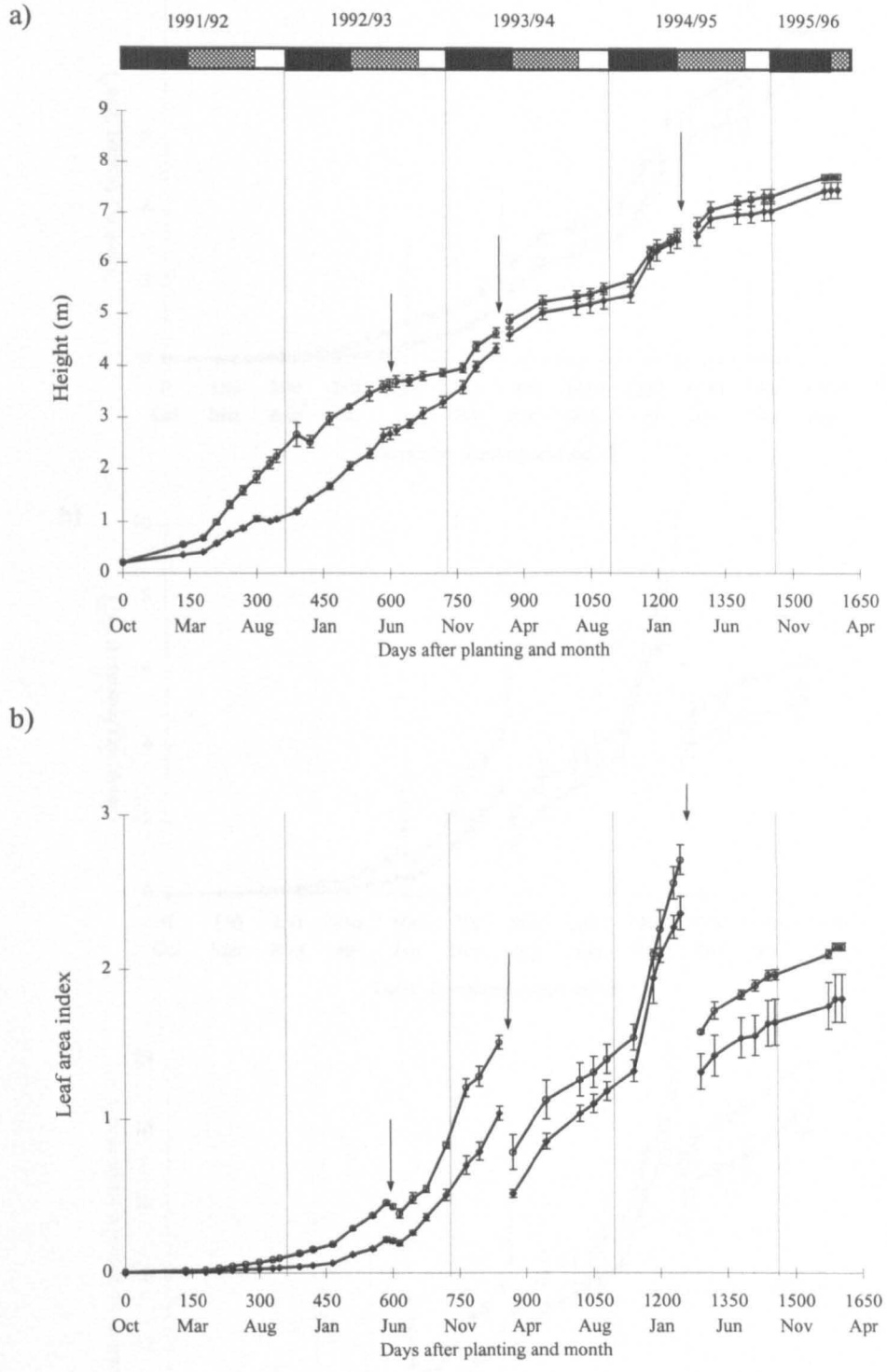


Figure 3.1 Time courses of a) mean tree height and b) mean leaf area index in the sole (Td; circles) and dispersed agroforestry (CTd; diamonds) treatments of grevillea from tree planting to the end of the experimental period. Arrows denote times of pruning and the horizontal bars represent seasons; black, short growing season (Oct-Feb); grey, long growing season (Mar-Jul); and open, dry season (Aug-Sep). Double standard errors of the mean are shown.

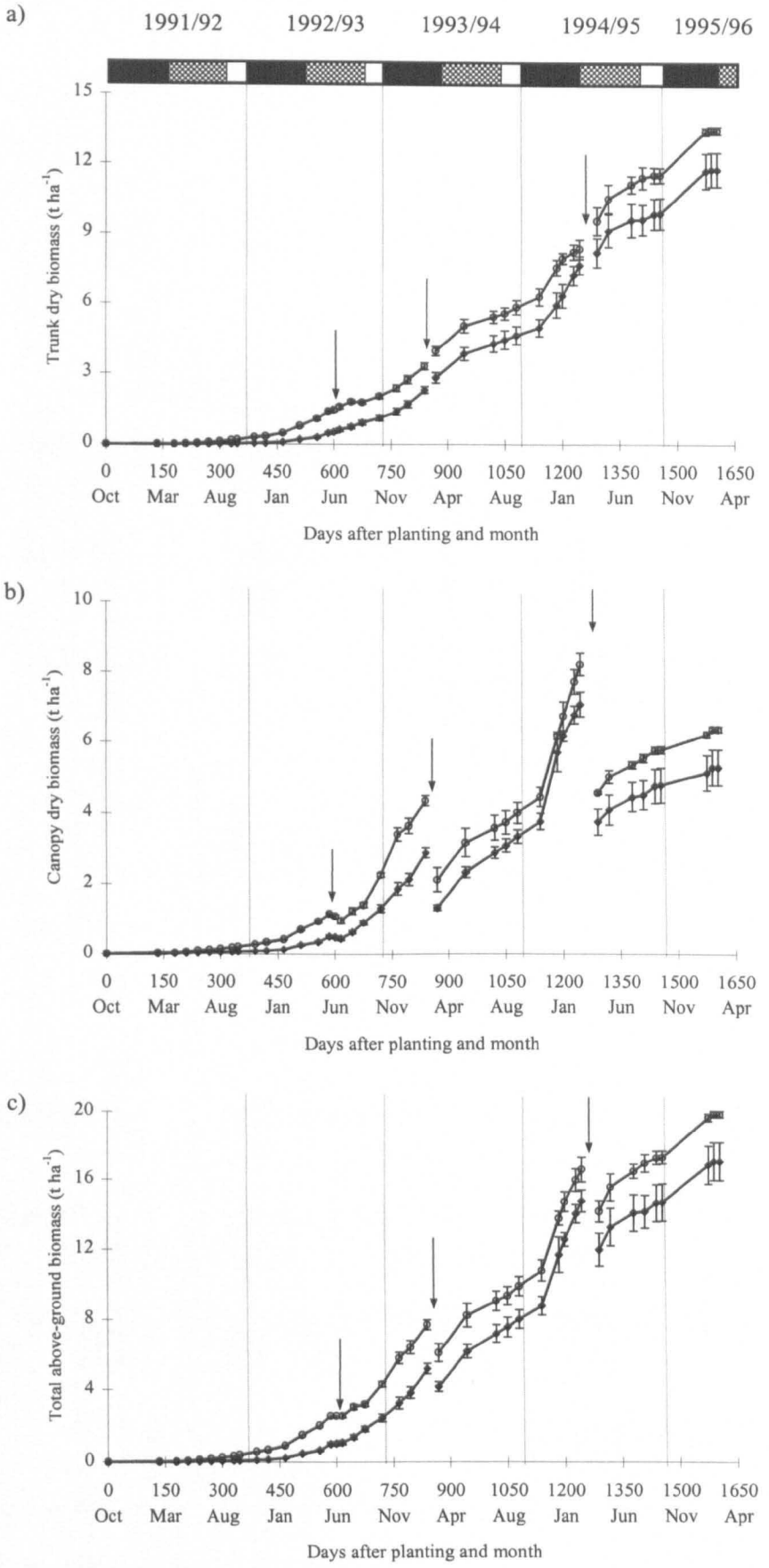
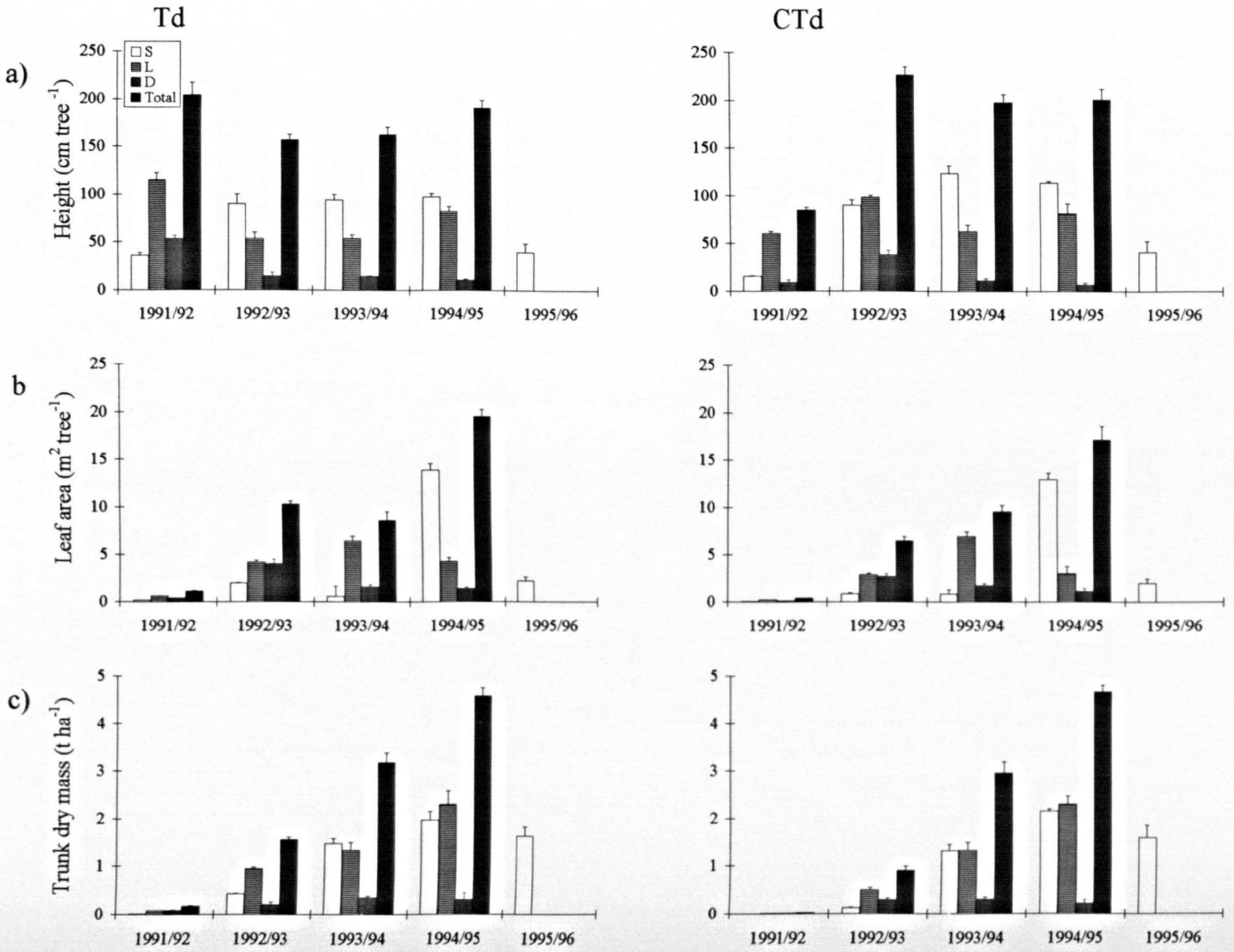


Figure 3.2 Time courses of a) trunk b) canopy and c) total above-ground biomass in the sole (Td; circles) and dispersed agroforestry (CTd; diamonds) treatments of grevillea from tree planting to the end of the experimental period. Arrows denote times of pruning and the horizontal bars represent seasons; black, short growing season (Oct-Feb); grey, long growing season (Mar-Jul); and open, dry season (Aug-Sep). Double standard errors of the mean are shown.


Td
CTd
a)
b
c)
S
L
D
Total
Height (cm tree -1)
Leaf area (m2 tree-1)
Trunk dry mass (t ha-1)
1991/92
1992/93
1993/94
1994/95
1995/96

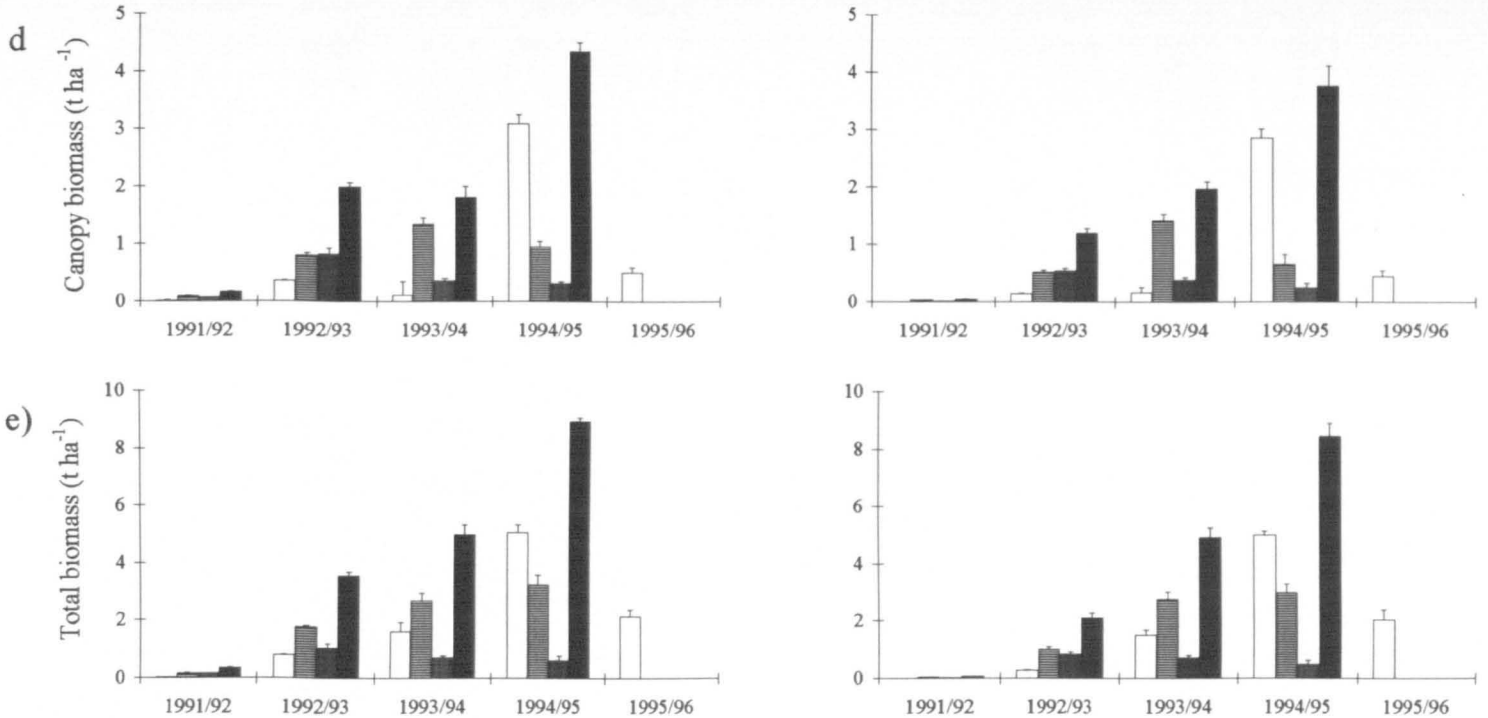
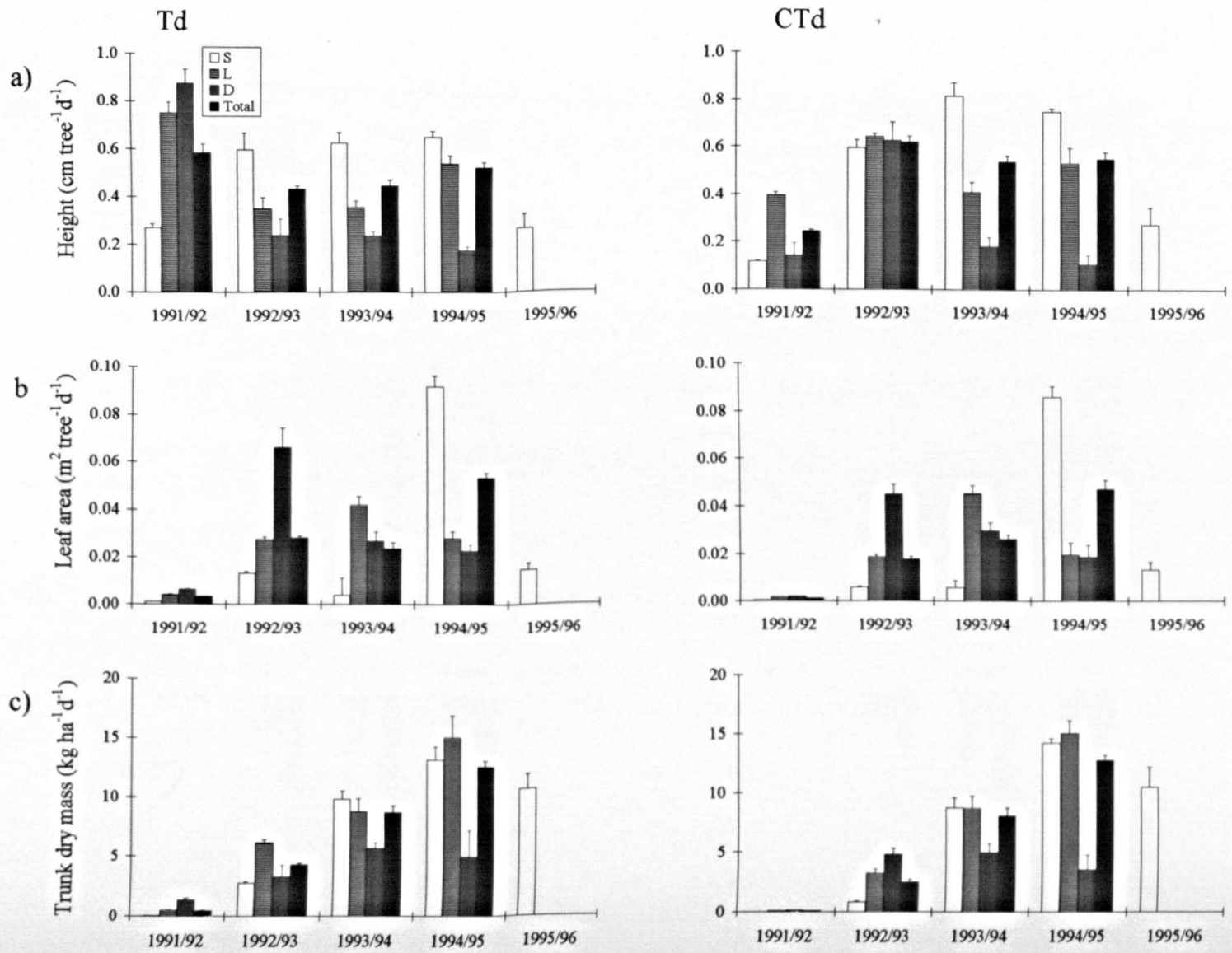


Figure 3.3 Seasonal and annual increments of a) height, b) leaf area and c) trunk, d) canopy and e) whole tree above-ground dry biomass of grevillea in the sole (Td) and dispersed agroforestry (CTd) treatments. S, L and D denote the short and long growing seasons and the dry season. Single standard errors of the mean are shown.


Td
CTd
a)
b
c)
S
L
D
Total
Height (cm tree-1 d-1)
Leaf area (m2 tree-1 d-1)
Trunk dry mass (kg ha-1 d-1)
1991/92
1992/93
1993/94
1994/95
1995/96

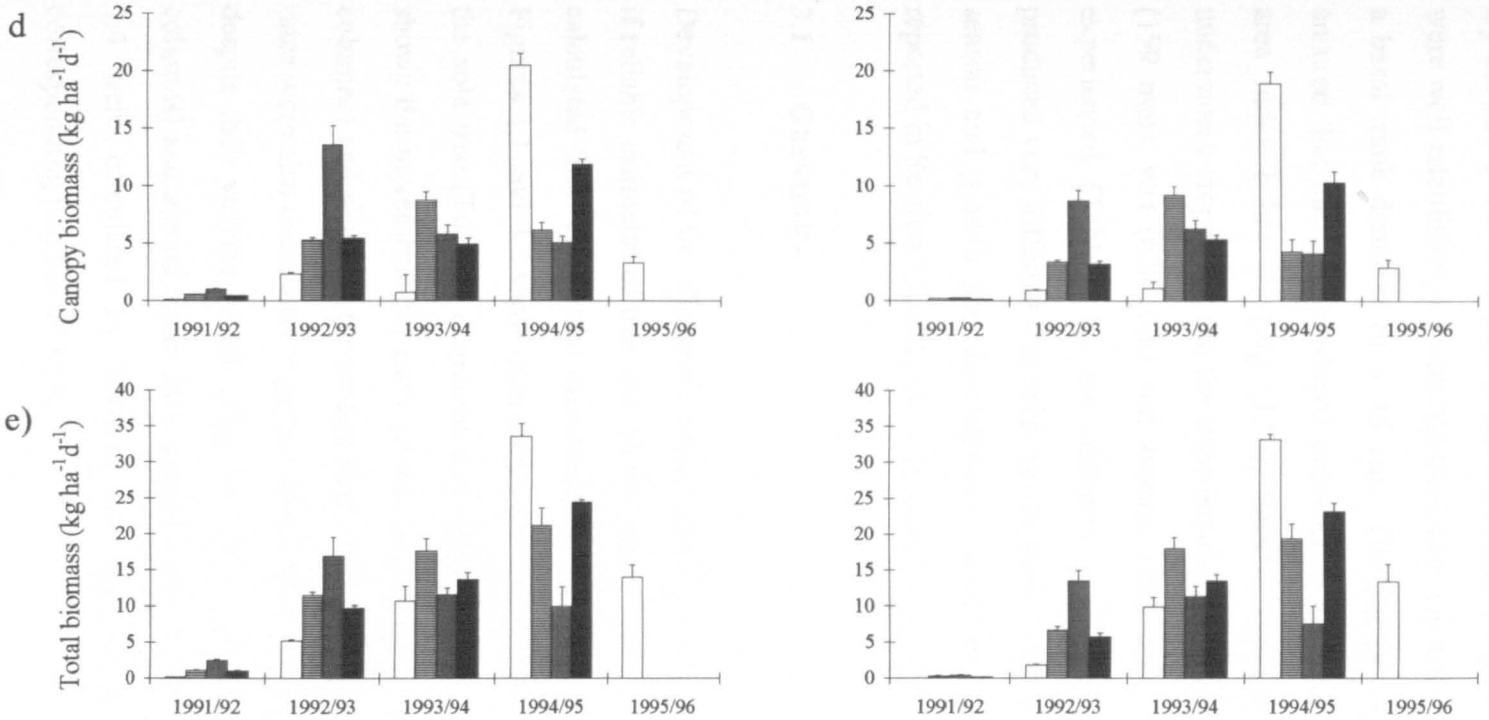


Figure 3.4 Seasonal and annual daily growth rate of a) height, b) leaf area and c) trunk, d) canopy and e) whole tree above-ground dry biomass of grevillea in the sole (Td) and dispersed agroforestry (CTd) treatments. S, L and D denote the short and long growing seasons and the dry season. Single standard errors of the mean are shown.

CHAPTER 3

GROWTH, BIOMASS ACCUMULATION AND LEAF AREA INDEX

By the end of the field studies reported here, the grevillea in the main CIRUS trial were well established 4.5 year old trees with a mean height of c. 8 m (Fig. 3.1a) and a basal trunk diameter of c. 15 cm. The regular pruning of the basal branches ensured that the trees produced unbranched trunks and generally maintained leaf area index below 2, (Fig. 3.1b), thereby avoiding excessive shading of the understorey crops. During the experimental period (L94 to S95/96), unusually dry (199 mm), wet (628 mm) and average (302 and 317 mm) rainy seasons were experienced (Table 2.1); the differing quantities and distribution of rainfall produced very different tree/crop interactions. Crop yields at final harvest for each season and growth and development during the main experimental period are reported in Section 3.2 and 3.3. The rapid tree growth is illustrated by Plate 3.1.

3.1 GREVILLEA

Development of the allometric procedures described in Section 2.4.1 was essential if reliable estimates of tree growth were to be obtained and resource use efficiency calculated from concurrent measurements of water use and radiation interception. Figures 3.1 and 3.2 show cumulative tree growth from planting to project end for the sole tree (Td) and dispersed agroforestry (CTd) treatments, while Figure 3.3 shows the increments for each growth parameter expressed on both annual (black columns) and seasonal timescales (open or hatched columns). Mean daily growth rates were also calculated to permit direct interseasonal comparisons of growth rate despite their varying length (Fig. 3.4). The values for seasonal (open or hatched columns) and annual mean daily growth rates (black columns) presented in Figure 3.4 were calculated by dividing the appropriate growth increment by the corresponding number of days.

Tree size, as assessed from measurements of height, leaf area index and biomass, was generally greater in sole grevillea (Td) than in the dispersed agroforestry

system (CTd; Figs. 3.1 and 3.2). Significant differences ($p<0.001$) between Td and CTd trees were established for all measured parameters during the first 130 days after planting (DAP), and only tree height (Fig 3.1a) consistently recovered to the sole tree values during the experimental period. The treatment differences in leaf area index and trunk, canopy and total above-ground biomass were sustained throughout the experimental period (Figs. 3.1 and 3.2) with the exception of brief periods, particularly during the unusually wet S94/95 season, when the differences were no longer statistically significant. The slower initial growth of the CTd grevillea probably resulted from water deficits caused by competition for water with the crops during tree establishment.

The more rapid initial growth of Td trees is clearly illustrated by the seasonal and annual increments and the corresponding mean daily growth rates for height, leaf area and above-ground dry biomass (Figs. 3.3 and 3.4). The seasonal increments and mean daily growth rates for all parameters except height were significantly greater in Td than in CTd trees ($p<0.05$) during 1991/92 and 1992/93, but thereafter there was no significant difference. The seasonal and daily height increments were significantly greater in the Td trees only during 1991/92 and thereafter were similar to or slightly lower than in the CTd treatment, thereby explaining the recovery of tree height in the CTd treatment to Td levels by January 1994. Tree heights were similar in both treatments for the remainder of the experimental period (Fig. 3.1). The annual height increment for Td grevillea was almost constant throughout the observation period (Fig. 3.3).

Forest mensurationists have suggested that tree height may be the most appropriate growth parameter for assessing productivity at specific sites (Zahner, 1968; Cannell, 1984). Thus, as tree height was similar for Td and CTd trees after 860 DAP, it might be concluded that productivity in the agroforestry system was similar to the sole stand from this point onwards. However, the sustained differences between treatments in leaf area and above-ground dry biomass (Figs. 3.1b and 3.2) resulting from the greater annual total and annual daily mean increments during the first two years in Td trees conflicts with the concept of using height to assess productivity. This is particularly pertinent to grevillea, for which the principal

economic return is as construction poles whose market value depends on their length and taper characteristics. Thus, while height increased more rapidly in CTd than in Td grevillea during 1992/93, this occurred at the expense of reduced assimilate allocation to support biomass accumulation in the trunk. As a result, the trunk volume and biomass of CTd trees never recovered fully to Td values during the observation period (Fig. 3.2). Peden *et al.* (1996) reached a similar conclusion in a study of 15 tree species, including grevillea, grown for poles in linear agroforestry systems and harvested 41 months after planting; they found that the poles produced by all species were inferior to those from commercial plantations in terms of their length and taper characteristics.

Mean daily height increments were generally greater during the short growing season than during the long growing season or dry season, resulting in the distinctive scalloping pattern shown by the timecourse for height (Fig. 3.1a) and to a lesser degree by the other growth parameters (Figs. 3.1b and 3.2). This seasonality of growth is found in many tree species (Zahner, 1962; Cannell, 1989), including evergreens, and is correlated with seasonal variation in soil water content and nutrient availability. The onset of the rains in October and the consequent increase in nutrient availability, particularly nitrogen (cf. Section 2.3), promoted a surge in growth, which then decreased gradually as nutrient and water supplies declined. In addition, mean, maximum and minimum temperatures were higher during the short growing season than during the long growing season or the dry season, although temperature rarely reached stress levels (cf. Table 2.2 and Section 4.1). Shortwave solar radiation receipts were also greater during the short growing season than during the long growing season (by 15 and 27 % in 1994/95 and 1995/96; Fig. 2.1). This combination of higher temperature and solar radiation receipts could be expected to promote more rapid growth. Growth continued during the dry season, sometimes at rates similar to or greater than during the cropping seasons. For example, the growth rates for leaf area, canopy biomass and total above-ground biomass in CTd trees were greater during the 1993 dry season than during the two preceding cropping seasons ($p<0.001$), with the result that the seasonal growth increment matched that recorded during the long growing season and was significantly higher than during the short growing season ($p<0.001$).

These observations suggest that the trees utilised residual soil water or deep reserves within the underlying friable bedrock during the dry season.

Canopy biomass and LAI increased rapidly in both Td and CTd grevillea at the beginning of the 1994/95 short growing season (Fig. 3.2b), during which rainfall was unusually high (628 mm). Neither variable differed significantly between treatments during this period, although the growth rate of the CTd trees declined below that of Td trees by the end of the season, and subsequently the canopy remained significantly smaller ($p<0.05$). A similar effect was observed for total above-ground biomass (Fig. 3.2c), although this was less pronounced because the consequent promotion of trunk growth was delayed until the following long rains (Fig. 3.4), even though rainfall was relatively low (302 mm) and canopy size had been reduced by pruning (Fig. 3.2). Thus the growth response of the trunk lagged behind that of the canopy, suggesting that trunk growth in established grevillea trees depends on the availability of assimilates and mineral reserves accumulated during preceding favourable seasons.

The view that water availability is the key to productivity in many tree species (Colie, 1952; Ralston, 1964; Cannell, 1989), particularly in the semi-arid tropics, is supported by Figure 3.5, which shows a strong positive correlation between the seasonal height increments of CTd and Td trees and total seasonal rainfall during 1994/95 and 1995/96 (CTd, $r^2 = 0.85$; Td, $r^2 = 0.81$). This relationship was less pronounced for the other growth parameters examined because pruning altered the relationship between accumulated biomass or leaf area and environmental variables. The r^2 values for tree height declined as the relationship was extrapolated progressively back through the experimental period to the 1991/92 short growing season, indicating that rainfall was a poor indicator of stem elongation during the early stages of tree growth. This was probably because the younger trees were less dependent on current rainfall as they were able to extract water from reserves present at depth in the soil profile or in the friable underlying bedrock. Parallel soil water balance studies by Institute of Hydrology staff indicated that these reserves became depleted as the trees grew larger, increasing their dependence on current rainfall for continued growth. In addition, water availability to the CTd trees in the

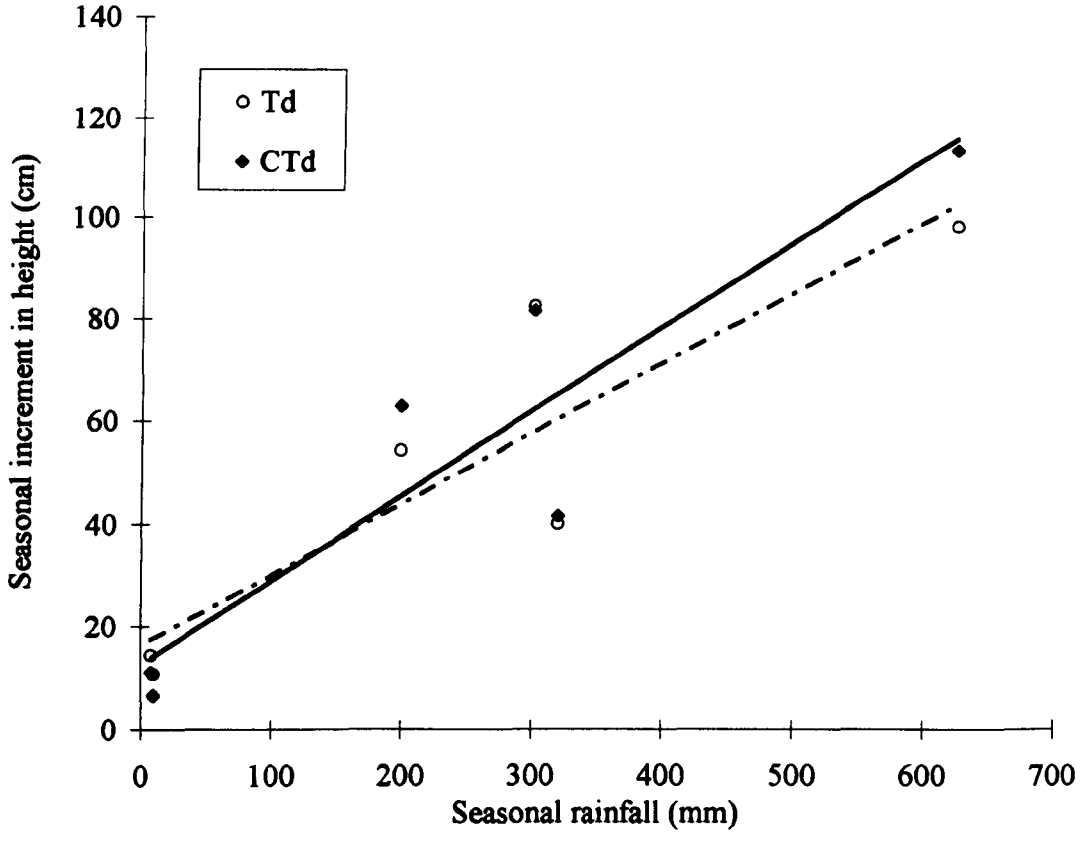


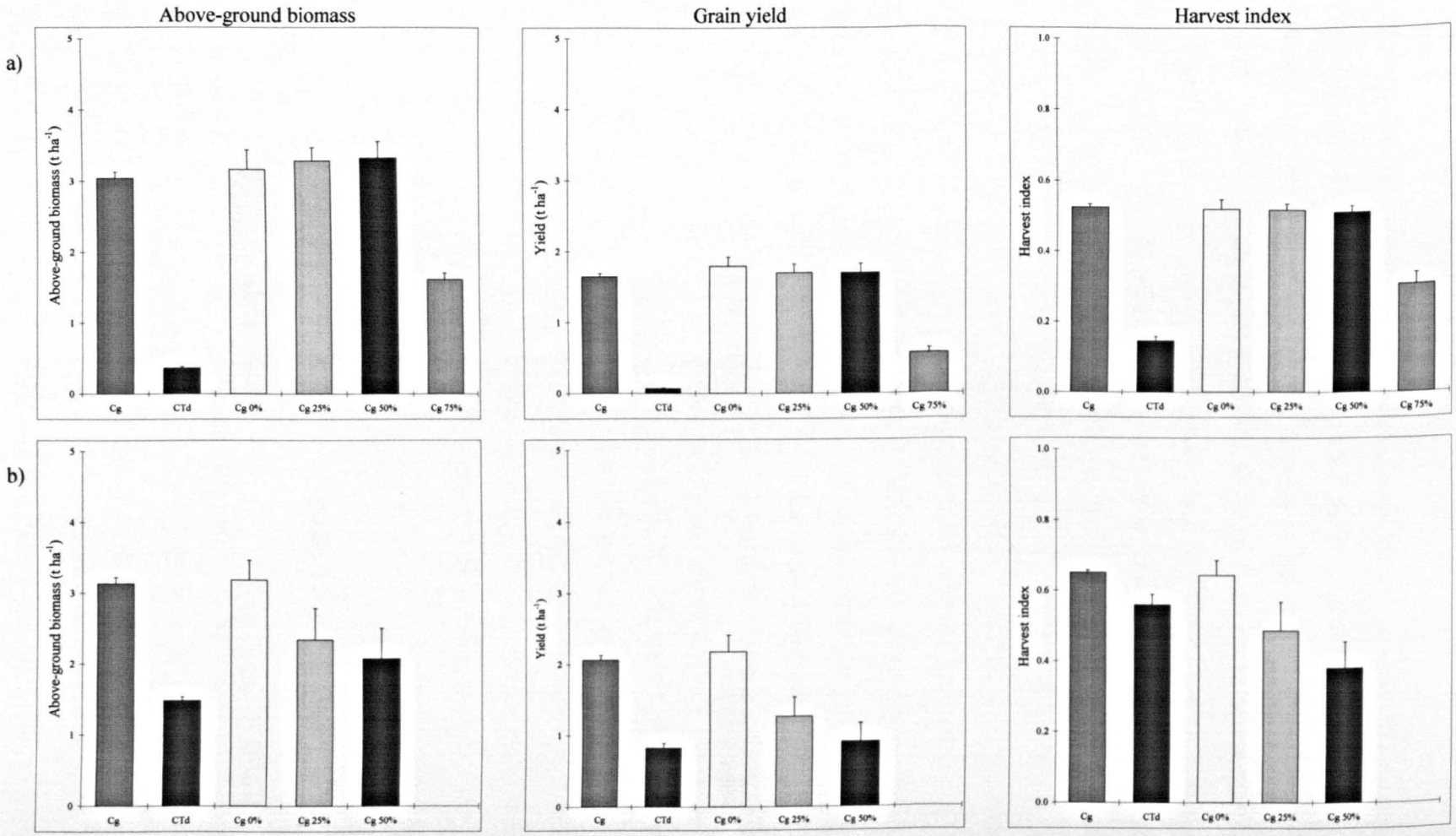
Figure 3.5 The relationship between seasonal accumulated growth in tree height and seasonal rainfall for grevillea in the sole (Td, dashed line, r^2 =0.81, n=6) or dispersed agroforestry (CTd, solid line, r^2 =0.85, n=6) treatments during the growing and dry seasons of the 1994/95 and 1995/96 experimental years.

surface horizons would have been limited by water extraction by the associated crop plants.

Shoot growth and dry matter accumulation in tree species are directly related to water availability (Wenger, 1952; Zahner, 1962). For example, Wenger found that shoot elongation was twice as great when the soil was allowed to dry to 60 % available water as opposed to 20 % available water after rewetting. In addition, Kozlowski (1964) concluded that water stress during the previous year affected shoot growth to a far greater extent than stress during the current year. Similarly, Zahner (1962) reported that stem growth in pine was reduced by 20 % during the first flush and by 100 % during the second flush as a result of drought in the preceding year. In CIRUS, competition from associated crops may have increased the frequency and severity of drought experienced by the CTd trees during the establishment period, the adverse effects of which appear to have persisted throughout the experimental period since neither tree biomass nor leaf area recovered to sole tree levels. However, correlation of seasonal tree growth with rainfall during the preceding season or year, or total rainfall during both the current and previous years, provided no improvement over the relationship for the current year shown in Figure 3.5. There may be two reasons for this: firstly, tree growth continued throughout the dry season, depleting residual soil water accumulated within the profile during the preceding rainy seasons that might otherwise have been used to sustain growth during growing seasons when rainfall was poor; and secondly, tree growth exhibited only a weak correlation with rainfall during the establishment period.

3.2 CROP GROWTH IN CIRUS

Figure 3.6 shows above-ground biomass, grain yield and harvest index at final harvest for maize in CIRUS for all seasons between the 1994 long and 1995/96 short rains (L94 to S95/96). These results clearly demonstrate the impact of intercropping with grevillea on the growth and productivity of maize. Above-ground biomass and grain yield were invariably greatly reduced in CTd maize and almost no yield was obtained in three of the four seasons; yield only reached c. 50


Above-ground biomass
Grain yield
Harvest index
a)
b)
Above-ground biomass (t ha-1)
Yield (t ha-1)
Harvest index
Cg
CTd
Cg 0%
Cg 25%
Cg 50%
Cg 75%

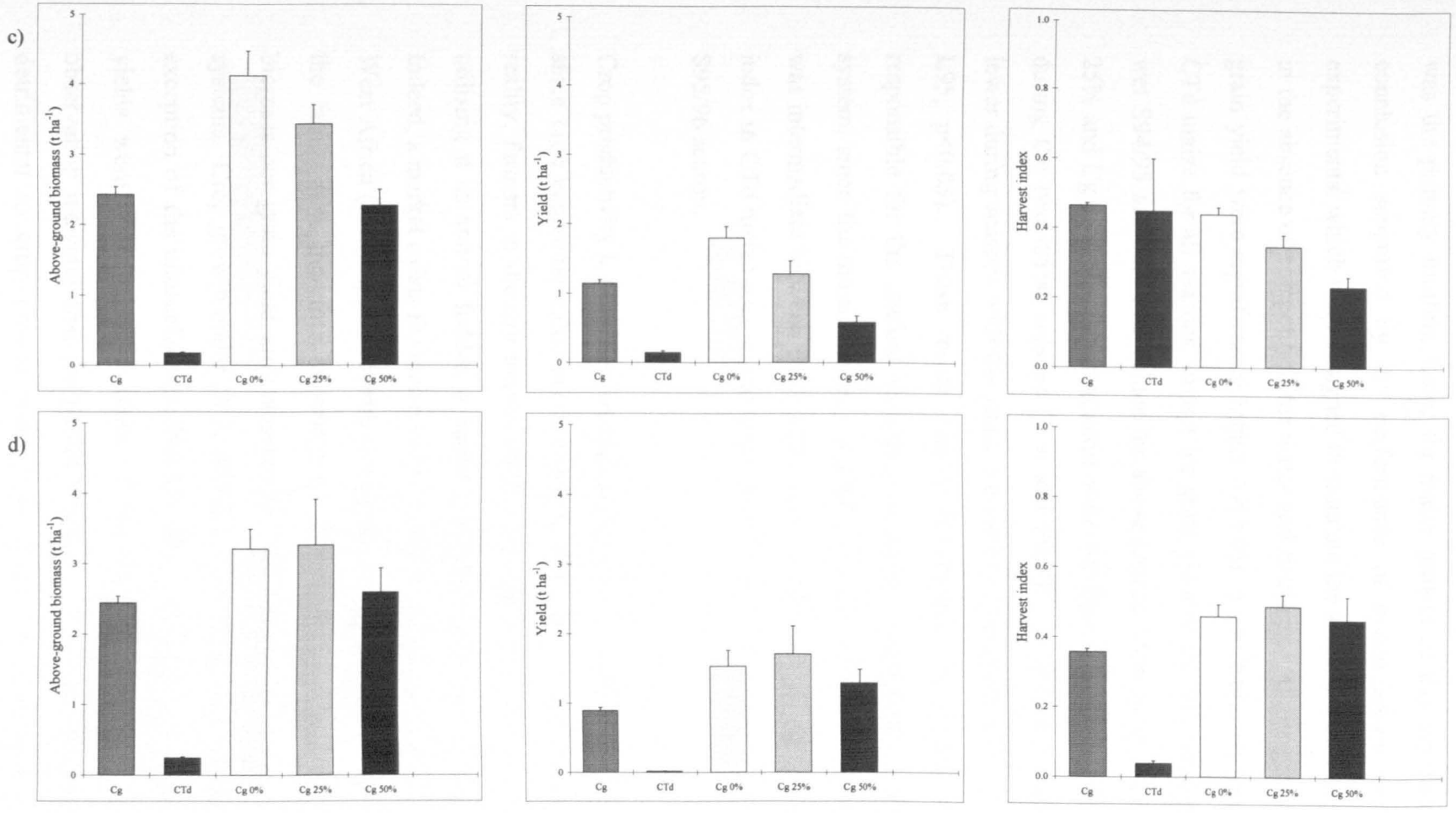


Figure 3.6 Above-ground biomass, grain yield and harvest index at final harvest of maize for a) long growing season 1994, b) short growing season 1994/95, c) long growing season 1995 and d) short growing season 1995/96. Data are shown for maize grown in the sole (Cg) or agroforestry (CTd) treatments, or as a sole crop under 0, 25 50 and 75% artificial shade (Cg 0%, Cg 25%, Cg 50% and Cg 75%). Single standard errors of the mean are shown.

% of that for sole maize when rainfall was much above average (628 mm *vs.* long-term average of 414 mm; Fig. 3.6b). These results suggest that water availability was the primary limiting factor for maize growth in this agroforestry system, a conclusion supported by the performance of maize grown in the shade net experiments, which were designed to simulate the shading effect of the tree canopy in the absence of competition for water and nutrients. Above-ground biomass and grain yield were significantly higher ($p<0.05$) in all shade net treatments than in CTd maize for all seasons, except for grain yield in Cg 50% during the unusually wet S94/95 season. The values for above-ground biomass and grain yield in Cg 25% and Cg 50% shading treatments were not significantly different from Cg 0% during the two driest seasons (L94 and S95/96; $p>0.05$) but were significantly lower during seasons with the greatest quantity of available soil water (S94/95 and L95; $p<0.05$). These results clearly demonstrate that shade was not solely responsible for the marked reduction in maize productivity in the agroforestry system, since the mean intensity of shading imposed on CTd maize by grevillea was intermediate between the Cg 25% and Cg 50% shade net treatments. Harvest index in CTd maize was less affected than biomass or grain yield in all except the S95/96 season.

Crop productivity is normally determined from the quantity of grain at final harvest, since crop economic value accrues mainly from grain production. However, in reality, farmers in the dry tropics attribute considerable value to maize stover by utilising it as animal fodder, a barrier against erosion (trash line), or as mulch. Indeed, a market exists for maize stover in many dryland areas of Kenya, India and West Africa (Franzel, pers. comm.), resulting in a net export of crop residues from the farm. It is therefore important for farmers that neither total above-ground biomass nor grain yield are compromised when crops are grown in agroforestry systems. Crop growth under 25 % artificial shade demonstrated that, with the sole exception of the unusually wet S94/95 season, above-ground biomass and grain yields were comparable to those of the unshaded Cg 0% treatment. This observation indicates that the partial shade cast by overstorey trees may not be detrimental to crop growth within this dryland environment and hence that productivity may, in principle, be increased by the introduction of appropriate tree

species. However, it is clear that the limitations imposed by below-ground competition must be minimised if farmers are seriously to consider adopting the technology.

Figure 3.7 shows results obtained from allometric measurements of leaf area index (LAI) and above-ground biomass for maize in the CTd and shade net treatments during the S94/95, L95 and S95/96 seasons. The timecourses extend to maturity for biomass but only to anthesis for leaf area, since the allometric relationship for determining leaf area (Section 2.4.2.1) could not be used once substantial leaf senescence had begun. The performance of CTd maize varied greatly between seasons; during the very wet S94/95 season (Fig. 3.7a), LAI and biomass were only slightly reduced relative to the Cg 50% shading treatment for much of the season (up to c. 90 DAS in the case of biomass). In contrast, both variables were drastically reduced in CTd maize during the drier L95 and S95/96 seasons (Plate 3.2a). Development was also delayed in CTd maize by c. 30 days relative to sole maize during the L95 and S95/96 seasons. This delay could not be solely attributed to the slower accumulation of thermal time under the trees (cf. Section 4.2.1) but may have originated because competition for soil moisture with the trees induced severe water stress (Plates 3.2b and 3.3). This conclusion is supported by the observation that the timing of flowering was similar in CTd and sole maize during the 1994/95 short growing season, when the unusually high rainfall alleviated water stress.

LAI and biomass decreased as shading intensity increased, although the magnitude of these effects again showed substantial inter-seasonal variation. The effects on LAI were invariably smaller than on biomass, especially during the relatively dry L95 season (Table 2.1), when biomass at maturity was reduced in the Cg 50% treatment by c. 50 % relative to the unshaded Cg 0% control, even though LAI was little affected prior to anthesis. LAI and above-ground biomass for Cg 0% maize were respectively 100 and 60 % greater during L95 than S95/96 despite the similar seasonal rainfall, although biomass at final harvest was only c. 30 % greater in L95 when plot level means were considered (Fig. 3.6). However, the greater vegetative growth during L95 did not result in proportionally higher grain yields (Fig. 3.6),

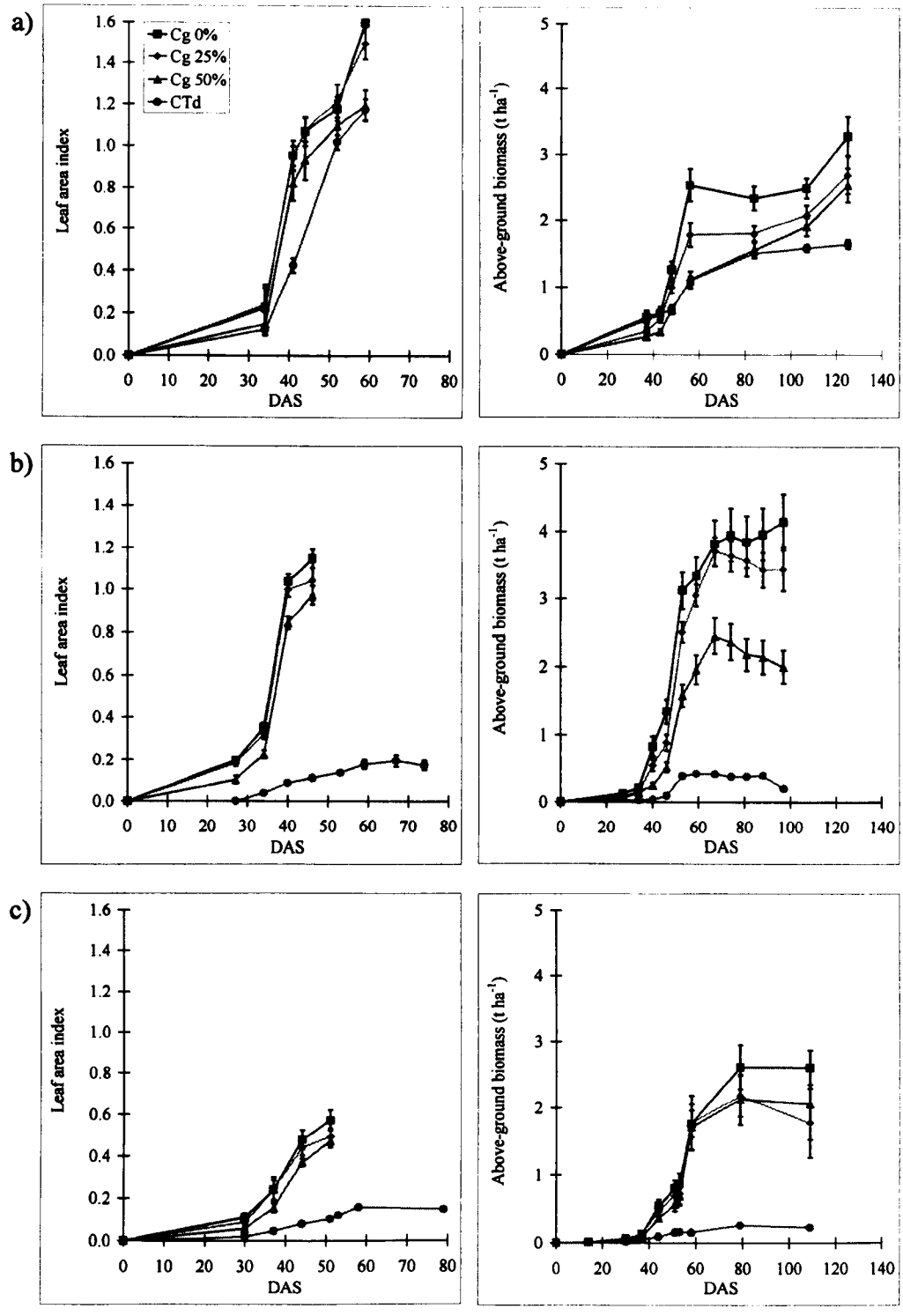


Figure 3.7 Timecourses of leaf area index and above-ground biomass for maize during a) short growing season 1994/95, b) long growing season 1995 and c) short growing season 1995/96. Data are shown for maize grown as a sole crop under 0 , 25 or 50 % artificial shade (Cg 0%, Cg 25% and Cg 50%) or in the agroforestry (CTd) treatment. Double standard errors of the mean are shown except when smaller than symbols.

Plate 3.2 (a; top left) Comparison of maize growth in neighbouring CTd and Cg plots and (top right) reduced maize growth near trees resulting from competition in the CTd treatment.

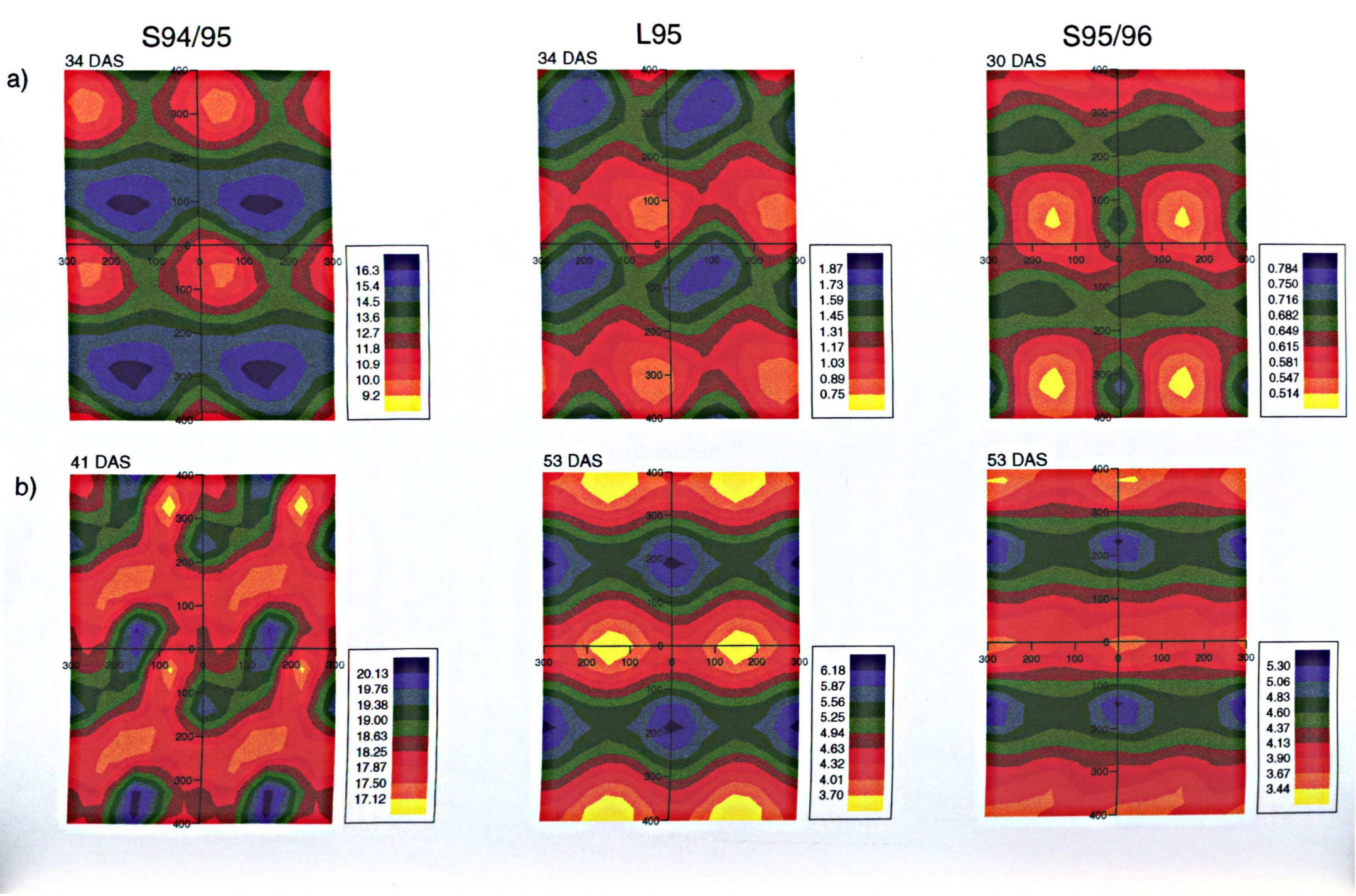
Plate 3.3 (b; bottom left) Impact of water stress on maize. Note the extensive leaf rolling to reduce surface area and radiation interception.

Plate 3.4 (c; bottom right) Line-planted grevillea in the Complementary Trial showing the delayed maturity of the cowpea under the tree rows resulting from the microclimatic amelioration provided by tree shade.

which was probably due to the distribution of rainfall. Copious rainfall was received during the early stages of the L95 season (Fig. 2.1), which therefore resulted in excessive vegetative growth. However, relatively little rainfall occurred during anthesis, silking and grain-filling (Fig. 2.1), causing the maize to become increasingly stressed during the reproductive phase. This was probably responsible for the observed shortening of the grain filling period by c. 10 days and is likely to have reduced both assimilate production and its translocation to the developing grain. Rainfall was more evenly distributed in S95/96, with sufficient being received during reproductive development to support grain filling and therefore despite greater above-ground biomass production during L95, maize yields were similar during both the S95/96 and L95 seasons.

Figures 3.8 and 3.9 show the spatial variation in leaf area and above-ground biomass at key developmental stages for maize in four adjacent cells of the CTd treatment during the S94/95, L95 and S95/96 seasons; the stages shown are panicle initiation, midway between panicle initiation and anthesis, anthesis and, for biomass, maturity. These figures illustrate the influence of proximity to the trees on maize performance in seasons with high (628 mm in S94/95) or average rainfall (302 and 317 mm in L95 and S95/96) and were plotted using the G-Sharp programme (Version 2.1, Advanced Visual Systems) from bilinearly interpolated values on a 33 by 33 grid. The north-south orientation roughly extends from the bottom right-hand corner to the top left-hand corner. It is important to note that, while unique keys have been used for each panel, increasing depth of colour from yellow to blue consistently shows an increase in the variable being examined. Values for leaf area and above-ground biomass were much higher in the unusually wet S94/95 season than in either of the other seasons examined.

Distance and orientation relative to the nearest tree clearly had major effects on maize performance which varied within and between seasons depending on climatic conditions and tree size. Leaf area and biomass generally increased with distance from the nearest tree (Plate 3.2b). Thus the area where maize performed best was generally located either in the centre of the cell (e.g. leaf area at 34 and 59 DAS in S94/95 and 79 DAS in S95/96; Figure 3.8), and biomass at 125 DAS in S94/95, 53


S94/95
L95
S95/96
a)
34 DAS
34 DAS
30 DAS
16.3
15.4
14.5
13.6
12.7
11.8
10.9
10.0
9.2
1.87
1.73
1.59
1.45
1.31
1.17
1.03
0.89
0.75
0.784
0.750
0.716
0.682
0.649
0.615
0.581
0.547
0.514
b)
41 DAS
53 DAS
53 DAS
20.13
19.76
19.38
19.00
18.63
18.25
17.87
17.50
17.12
6.18
5.87
5.56
5.25
4.94
4.63
4.32
4.01
3.70
5.30
5.06
4.83
4.60
4.37
4.13
3.90
3.67
3.44

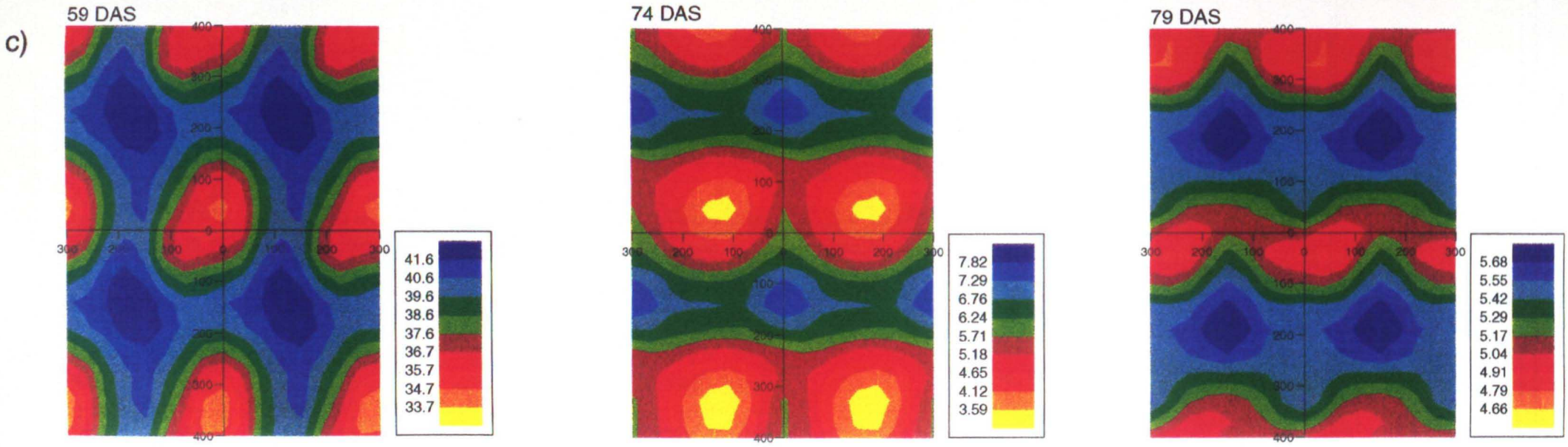
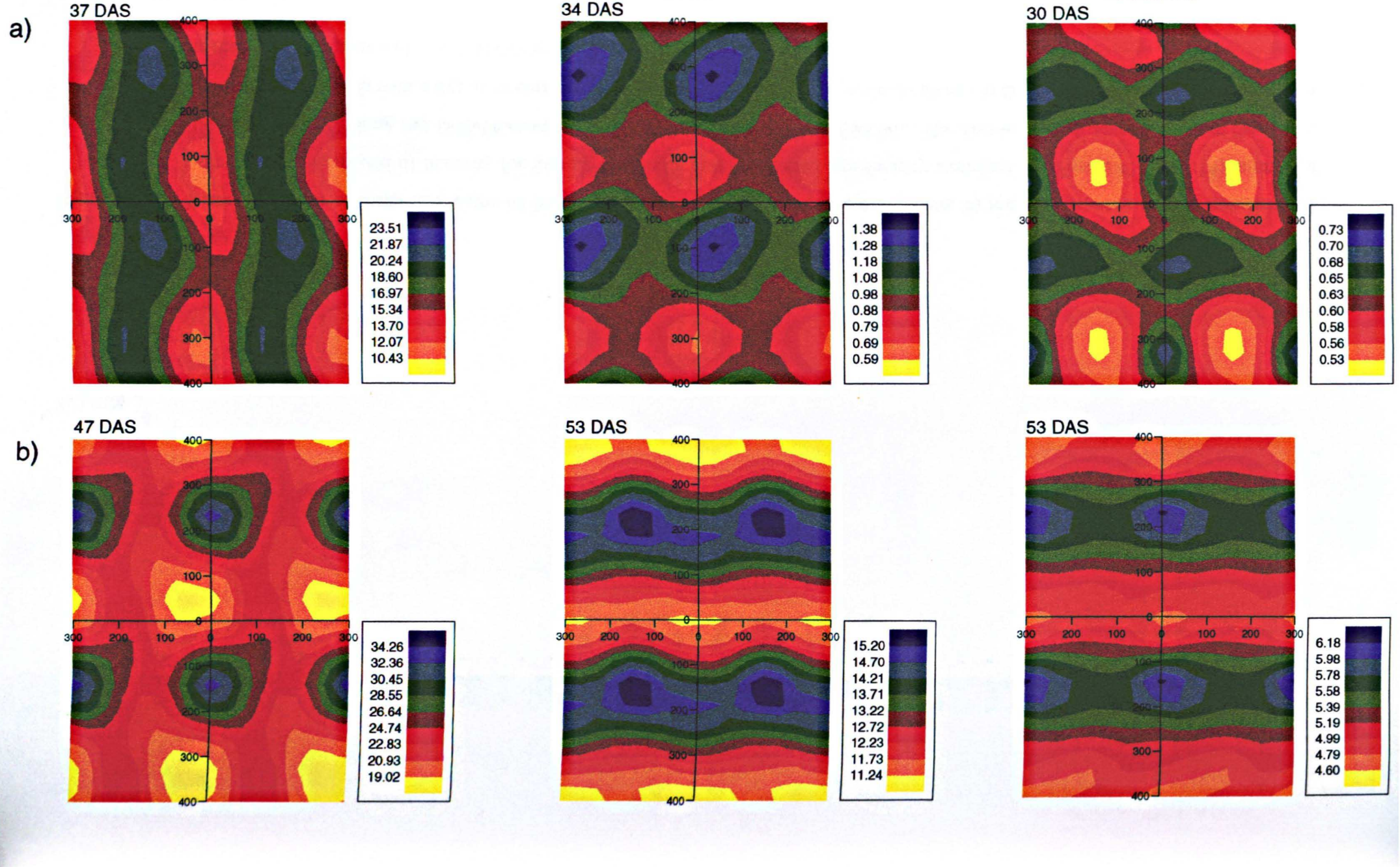


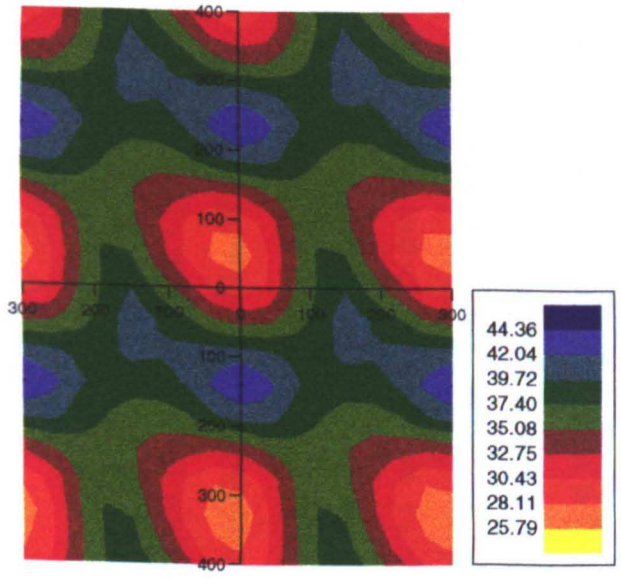
Figure 3.8 Spatial variation of mean leaf area (dm^2) in maize at a) panicle initiation, b) midway between panicle initiation and anthesis, and c) anthesis, for four adjacent cells in the dispersed agroforestry treatment (cf. Figs. 2.13 and 2.14) during the 1994/95 short, 1995 long and 1995/96 short growing seasons (S94/95, L95 and S95/96). The axes indicate distance (cm) from the central tree of four cells, each with a tree at its corners. Each panel has its own unique scale, as shown in the keys.

Figure 4.9 Spatial variation of mean above-ground biomass (g DW) in maize at a) panicle initiation, b) midway between panicle initiation and anthesis, c) anthesis and d) maturity for four adjacent cells in the dispersed agroforestry treatment (cf. Figs. 2.13 and 2.14) during the 1994/95 short, 1995 long and 1995/96 short growing seasons (S94/95, L95 and S95/96). The axes indicate distance (cm) from the central tree of four cells, each with a tree at its corners. Each panel has its own unique scale, as shown in the keys. (Figure 4.9 can be found on the reverse of this page and on the adjoining page).

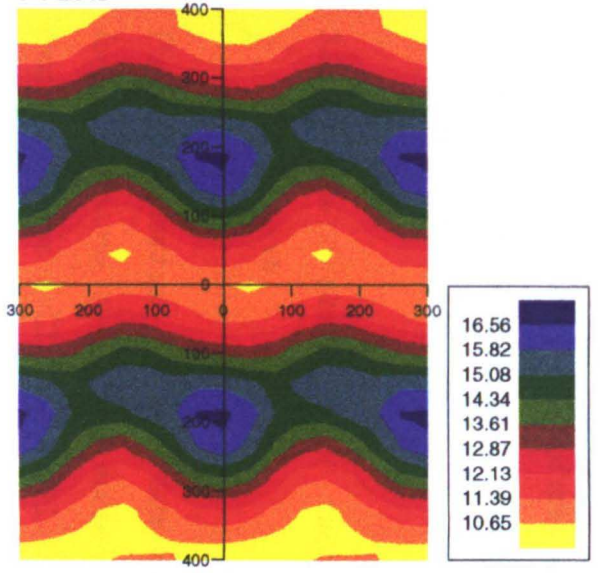

S94/95
L95
S95/96
a)
37 DAS
34 DAS
30 DAS
23.51
21.87
20.24
18.60
16.97
15.34
13.70
12.07
10.43
1.38
1.28
1.18
1.08
0.98
0.88
0.79
0.69
0.59
0.73
0.70
0.68
0.65
0.63
0.60
0.58
0.56
0.53
b)
47 DAS
53 DAS
53 DAS
34.26
32.36
30.45
28.55
26.64
24.74
22.83
20.93
19.02
15.20
14.70
14.21
13.71
13.22
12.72
12.23
11.73
11.24
6.18
5.98
5.78
5.58
5.39
5.19
4.99
4.79
4.60

c)

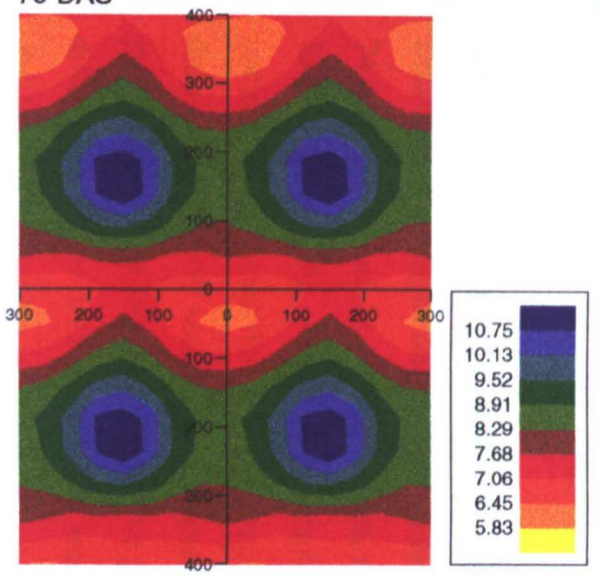
56 DAS



74 DAS

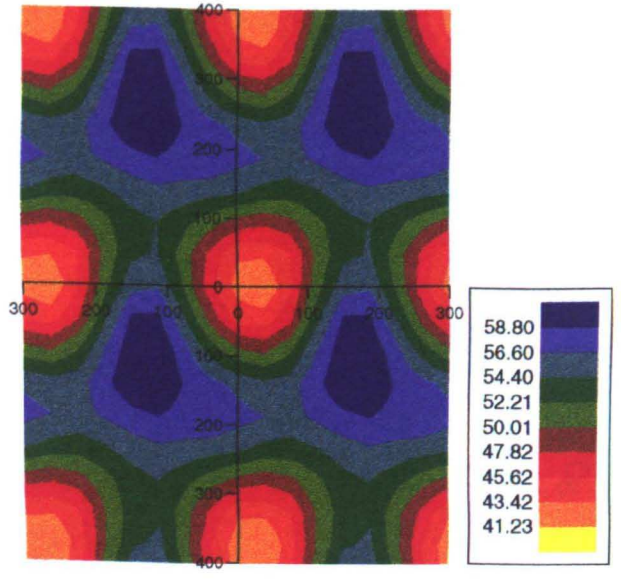


79 DAS

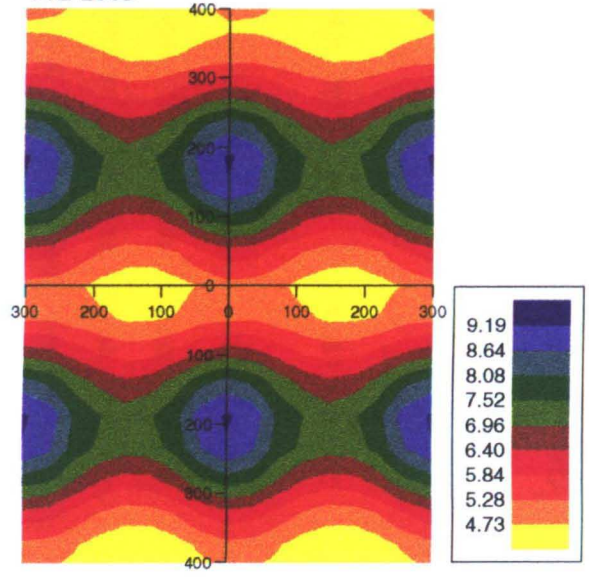


d)

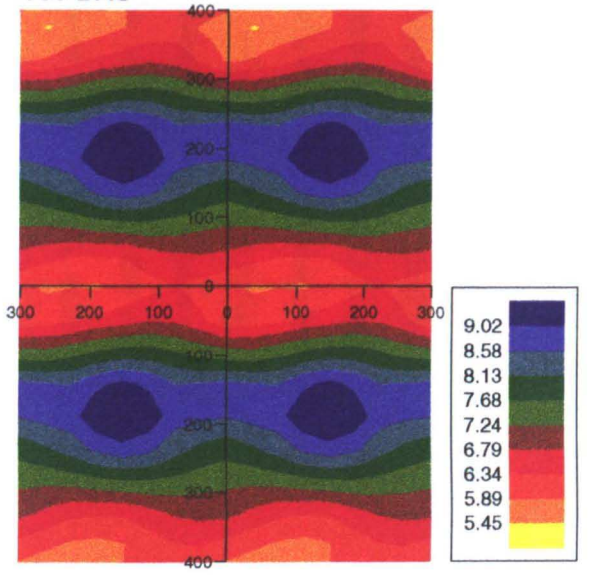
125 DAS



112 DAS



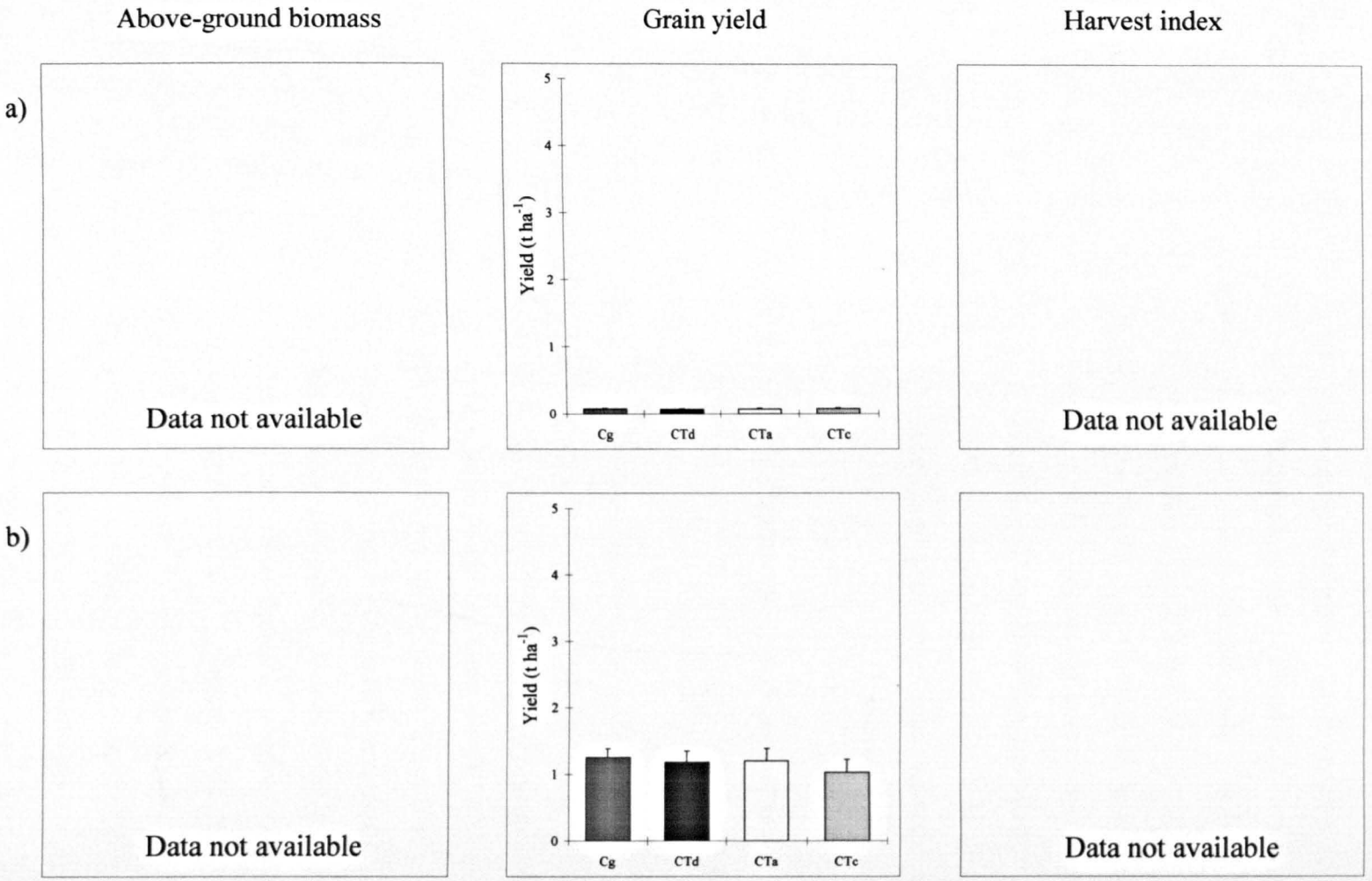
109 DAS



DAS in L95 and 79 and 109 DAS in S95/96; Figure 3.9) or midway between trees situated on the longer axis of the dispersed tree arrangement (e.g. leaf area at 53 and 74 DAS in L95 and 53 DAS in S95/96, and biomass at 74 and 112 DAS in L95 and 53 DAS in S95/96). Although the origin of these changing tree/crop interactions is unclear, it is apparent that crop performance varied greatly within cells, even during the very wet S94/95 season when biomass at maturity was 43 % greater at the most productive than at the least productive position within the cell; the corresponding differences for the L95 and S95/96 seasons were 94 and 66 %, even though the absolute values for biomass were much lower. Information of this type, together with allied information on spatial variation in incident radiation, temperature and other microclimatic variables (cf. Chapter 4), will be invaluable in the evolution and testing of effective models of resource capture and productivity in agroforestry systems, such as those being developed under the DFID Agroforestry Modelling Programme (cf. Section 1.5).

3.3 GROWTH RESPONSE OF CROPS WITH DIFFERING PHOTOSYNTHETIC PATHWAYS

Figure 3.10 illustrates final yield data, collected by S.B. Howard (Howard, 1997), for the alternating cowpea and maize crops grown during four of the first five cropping seasons in CIRUS (S91/92-S93/94); lack of rain caused complete crop failure in L93. Grain yield did not differ significantly between treatments during the first three seasons despite the rapid tree growth and widely varying seasonal rainfall. Treatment effects only became apparent for cowpea during S93/94, when above-ground biomass and grain yield were significantly higher ($p<0.001$) in Cg than in CTd cowpea, although it is conceivable that the extremely high rainfall during the S92/93 season (773 *vs.* long-term average of 414 mm) minimised the competitive impact of the trees in the CTd system. These results clearly demonstrate the complicating influence of substantial inter-seasonal variation in rainfall in studies where the performance of different species are to be compared in consecutive growing seasons, and lend support to the decision to grow maize continuously in the main CIRUS trial and establish the Complementary trial to enable comparisons of maize and cowpea to be made within the same season.


Above-ground biomass
Grain yield
Harvest index
a)
b)
Data not available
Data not available
Data not available
Yield (t ha-1)
0
1
2
3
4
5
Cg
CTd
CTa
CTc
Data not available
Data not available
Data not available
Yield (t ha-1)
0
1
2
3
4
5
Cg
CTd
CTa
CTc

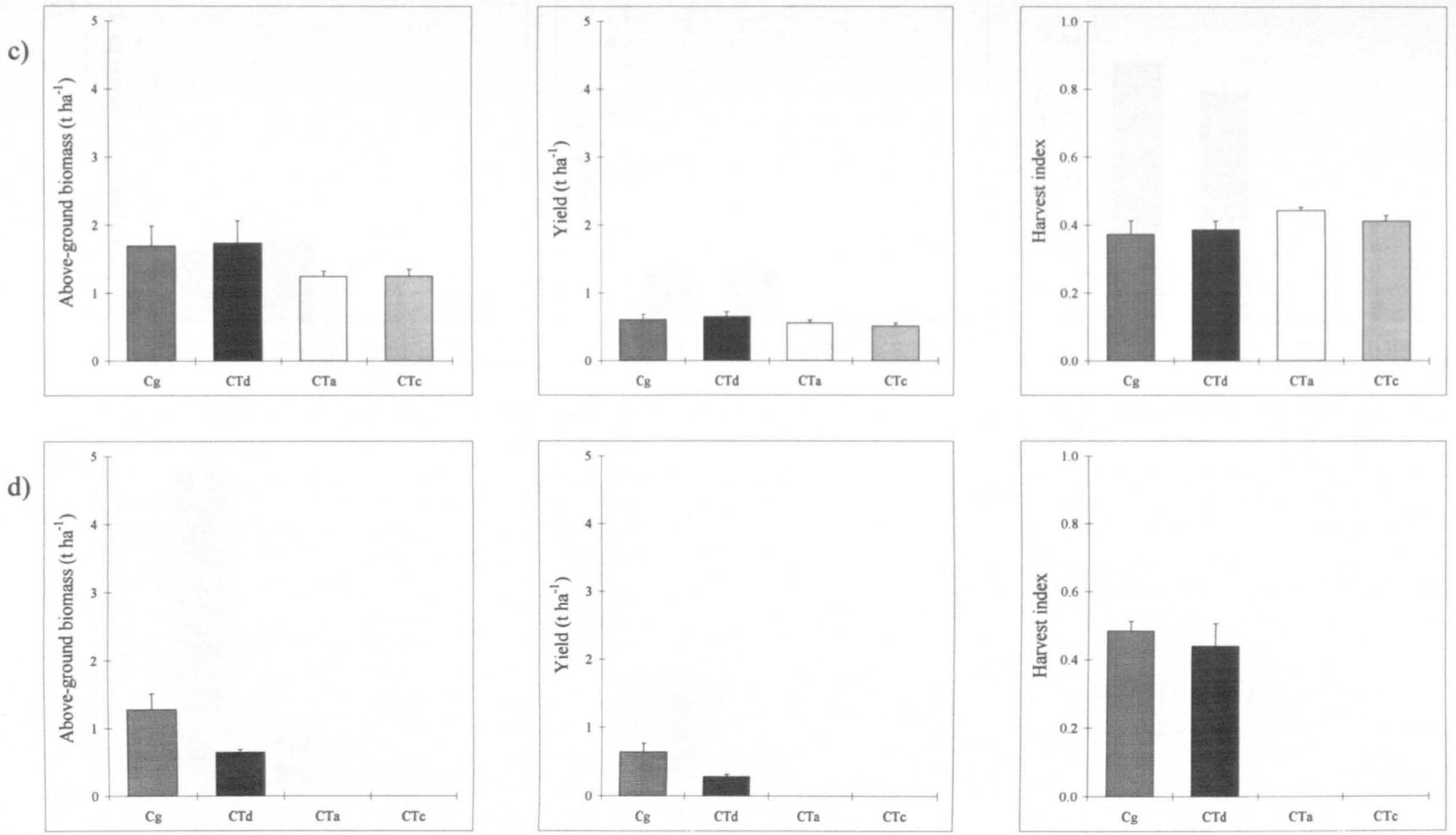


Figure 3.10 Grain yield at final harvest for a) the short growing season 1991/92 (cowpea) and b) the long growing season 1992 (maize), and above-ground biomass, grain yield and harvest index for c) short growing season 1992/93 (cowpea) and d) short growing season 1993/94 (cowpea). Data are shown for maize and cowpea grown as sole stands (Cg) and in agroforestry systems with dispersed (CTd), across contour (CTa) and contour (CTc) tree arrangements. The axis are equivalent to those in Figure 3.6 to allow easy comparison of data and single standard errors of the mean are shown.

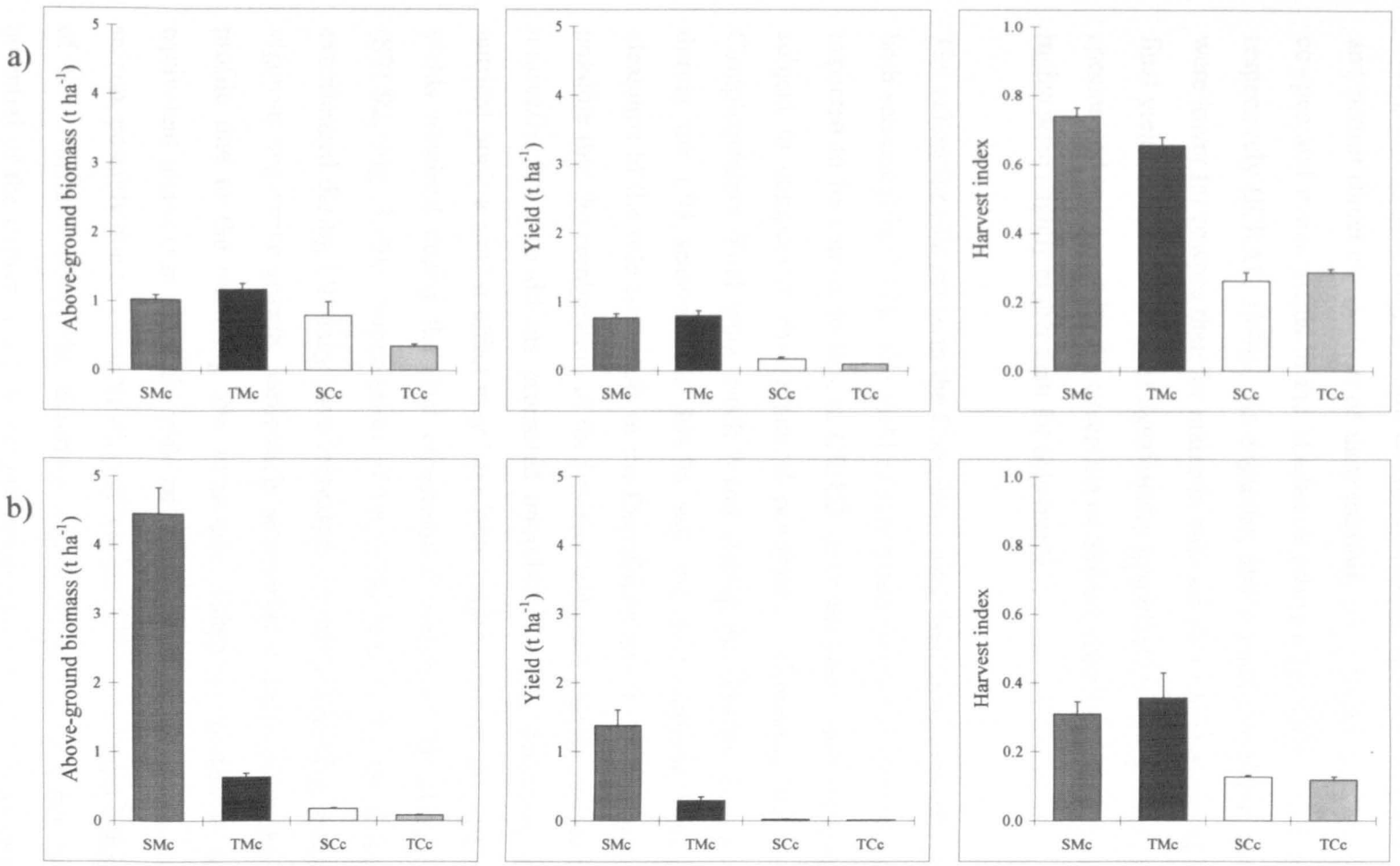


Figure 3.11 Above-ground biomass, grain yield and harvest index at final harvest of maize and cowpea for a) the short growing season 1994/95 and b) the long growing season 1995. Data are shown for maize and cowpea grown either as sole stands (SMc and SCc respectively), or in the dispersed agroforestry treatment (TMc and TCc respectively) in the Complementary Trial. Single standard errors of the mean are shown.

The harvest data for the Complementary trial (Fig. 3.11) illustrate the impact of grevillea on crops with contrasting photosynthetic pathways and potentially differing responses to shade. The data are for two seasons when maize and cowpea were grown concurrently to eliminate inter-seasonal variation in growing conditions and permit direct comparison of their performance. Under unstressed conditions, cowpea and maize yields in the Machakos area are typically c. 1.8 and 4.5 t ha^{-1} respectively (ICRAF, 1994). As expected, above-ground biomass and grain yield were lower for cowpea than for maize in both seasons. Above-ground biomass and final yield were reduced in the agroforestry treatment relative to sole crops for both species and seasons, with the exception of S94/95 when the values for intercropped maize were slightly higher than for sole maize.

The values for sole maize in the Complementary Trial were somewhat surprising in both seasons (Fig. 3.11). The yield of sole maize in the Complementary Trial was expected to be similar to that in CIRUS since the sites were adjacent and hence subject to comparable environmental conditions. However, the values for the Complementary Trial were much lower during the S94/95 season, but greater during the L95 season. As S94/95 was the first cropping season following clearance of the sole crop plots in the Complementary Trial in August 1994, it is possible that the combination of the initially high soil organic matter content with unusually moist conditions promoted microbial activity, depleting the available nutrient pool; a similar effect may have been responsible for the very low cowpea yields obtained during the first experimental season in the main CIRUS trial (S91/92; Fig. 3.10). Suppression of microbial activity by the drier conditions experienced during L95 may have increased nutrient availability, promoting more vigorous vegetative growth, particularly as residual moisture remained deep in the profile due to the relatively low extraction during the preceding season. An equivalent increase in the grain yield of sole maize was not observed during this season, possibly due to a combination of low rainfall during grain filling, depletion of soil moisture during the luxuriant vegetative phase, and the limited yield potential of the cultivar used, Katumani composite, which only produces one cob per plant; this genetically determined trait sets a ceiling on yield irrespective of growing conditions.

Because of the complicating influence of possible differences in soil nutrient status and organic matter content between the sole and agroforestry plots in the Complementary Trial resulting from their different clearance dates (August 1994 and March 1992 respectively), the performance of understorey maize in the Complementary Trial was compared with that of sole maize in CIRUS, which had been established only nine months earlier (October 1991) than the agroforestry plots in the Complementary Trial. Equivalent sole cowpea plots were not available because of the decision to grow maize continuously in CIRUS. Cowpea was less affected than maize by competition with grevillea since final grain yields were reduced by 43 and 30 % during the two seasons examined, compared to 64 and 75 % in maize, probably because the delayed senescence of cowpea in the agroforestry treatment extended the growing season (Plate 3.4). Total above-ground biomass was consistently reduced by c. 50 % in both species with the exception of maize during the very wet S94/95 season, when the observed yield reduction of 75 % was 20 % greater than in the main CIRUS trial.

3.4 COMPLEMENTARITY OF RESOURCE USE AND SYSTEM PRODUCTIVITY

To assess species performance in the agroforestry treatment (CTd) relative to the sole tree and crop stands (Td, Cg), performance ratios were calculated for both components as:

$$PR_i = \frac{M_a}{M_s} \qquad \text{Equation 3.1}$$

where PR_i is the performance ratio for grevillea, M_a represents the total above-ground biomass of the trees (t ha^{-1}) in the CTd treatment and M_s is the equivalent value for the Td treatment. In order to calculate performance ratios solely for the dry biomass within the grevillea trunks (PR_w), M_a and M_s in Equation 3.1 were replaced with the appropriate values for trunk dry biomass in the CTd and Td treatments. Performance ratios were calculated for maize and cowpea on the basis of both grain yield (PR_g) and total above-ground biomass (PR_b) using Equation 3.1 and substituting the relevant values. PR_i was very low (0.14) during the first cropping season (S91/92), but thereafter increased steadily to reach unity by L94; similar values were obtained for all subsequent cropping seasons and dry seasons (Fig. 3.12a). PR_w followed a similar pattern, although rapid

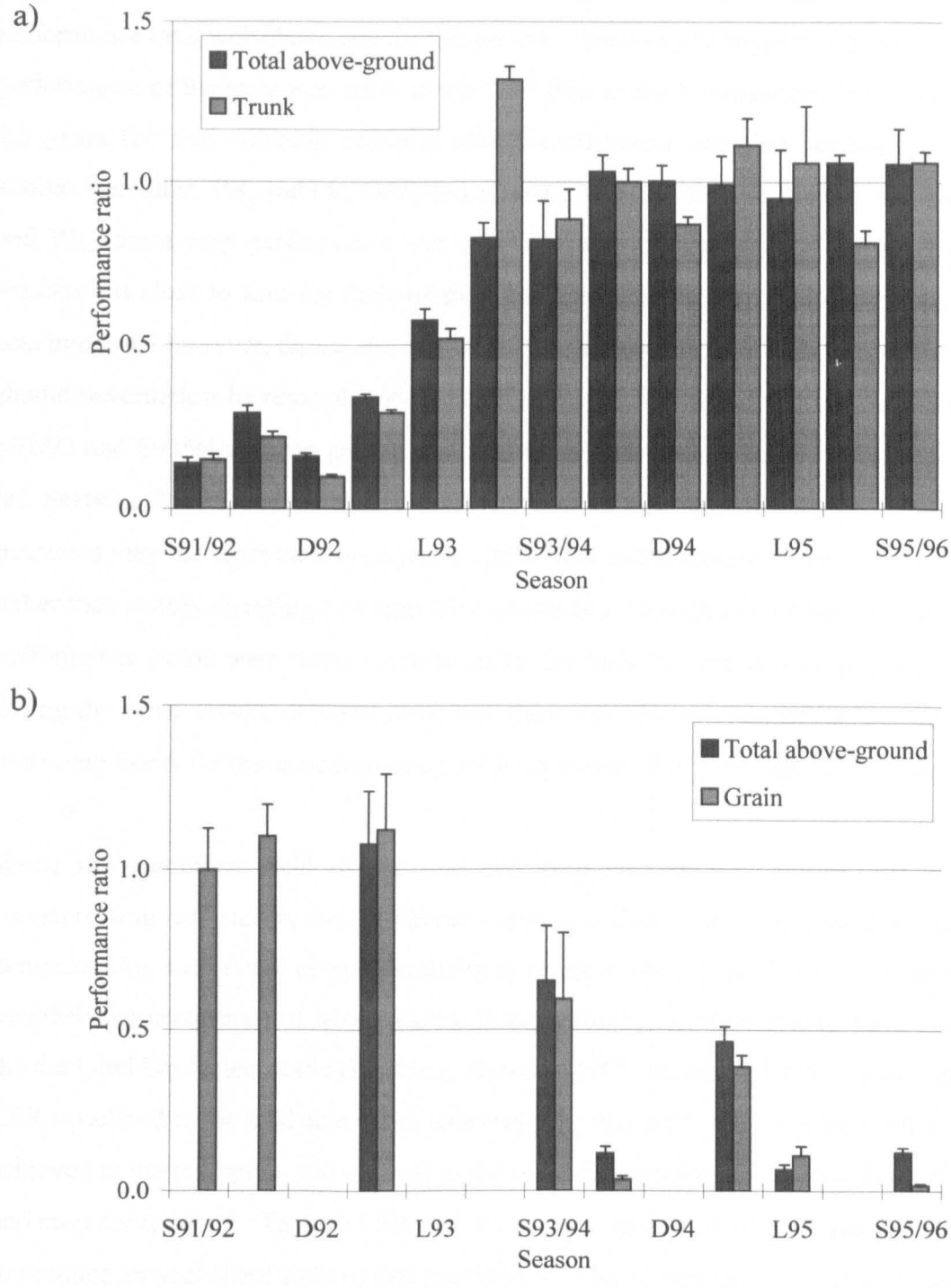


Figure 3.12 Seasonal and annual performance ratios for the dispersed agroforestry (CTd) treatment calculated for a) total above ground biomass and trunk biomass of grevillea and b) total above ground biomass and grain yield of the crop. Single standard errors of the mean are shown.

growth of the trunks in the CTd treatment during the 1993 dry season resulted in a performance ratio well above one for this period. These results suggest that the seasonal performance of the trees was lower in the CTd than in the Td treatment during the first 2.5 years (or five cropping seasons) after establishment and that performance was similar thereafter. PR_g and PR_b exhibited almost exactly the reverse trend to that for PR_t and PR_{tt}, since crop performance was close to unity during the first three cropping seasons but close to zero for three of the final four seasons (Fig. 3.12b). Performance was improved however, during the very wet S94/95 season ($PR_g = 0.39$; $PR_b = 0.46$). It should nevertheless be remembered that in three of the four successful seasons between S91/92 and S93/94 the crop grown was cowpea, and that maize was subsequently used (cf. Sections 2.4.2.2 and 3.3). The dramatic decline in crop performance in the CTd treatment may therefore have been partly attributable to the change in the species grown rather than simply changing tree/crop interactions as a consequence of tree growth. The performance ratios were never close to unity for both the tree and crop components during the same season, demonstrating that there was always competition between the two components for the same resource pool irrespective of crop species or tree size.

When the combined yield of the tree and crop components exceeds that of the corresponding sole stands, the agroforestry system is described as over-yielding, and is demonstrating a degree of complementarity in resource use (cf. Section 1.1). In order to establish the occurrence of over-yielding in agroforestry, various authors have utilised the the Land Equivalent Ratio (LER; e.g. Howard, 1997; Marshall, 1995; Corlett, 1989). LER is defined as the land area under sole cropping that is required to produce the yield achieved in intercropping, and is equal to the sum of the performance ratios for both tree and crop components. Thus an LER of 1.2 indicates that 1.2 ha of sole crop is required to produce an equivalent yield to that provided by 1 ha of intercrop. As LER values are strongly affected by the growing environment, it is essential that the mixtures and sole stands are formulated so as to optimise the performance of each community (Loomis and Conner, 1992; Howard, 1997). It is therefore conceivable that the densities of one or both of the component species may differ between the sole and intercrop. However, it has been suggested that this proviso has not been adhered to in many studies, seriously undermining the relevance of the values obtained for LER (Loomis and Connor, 1992; Rao and Coe, 1992). The tree and crop components of the CTd treatment in CIRUS

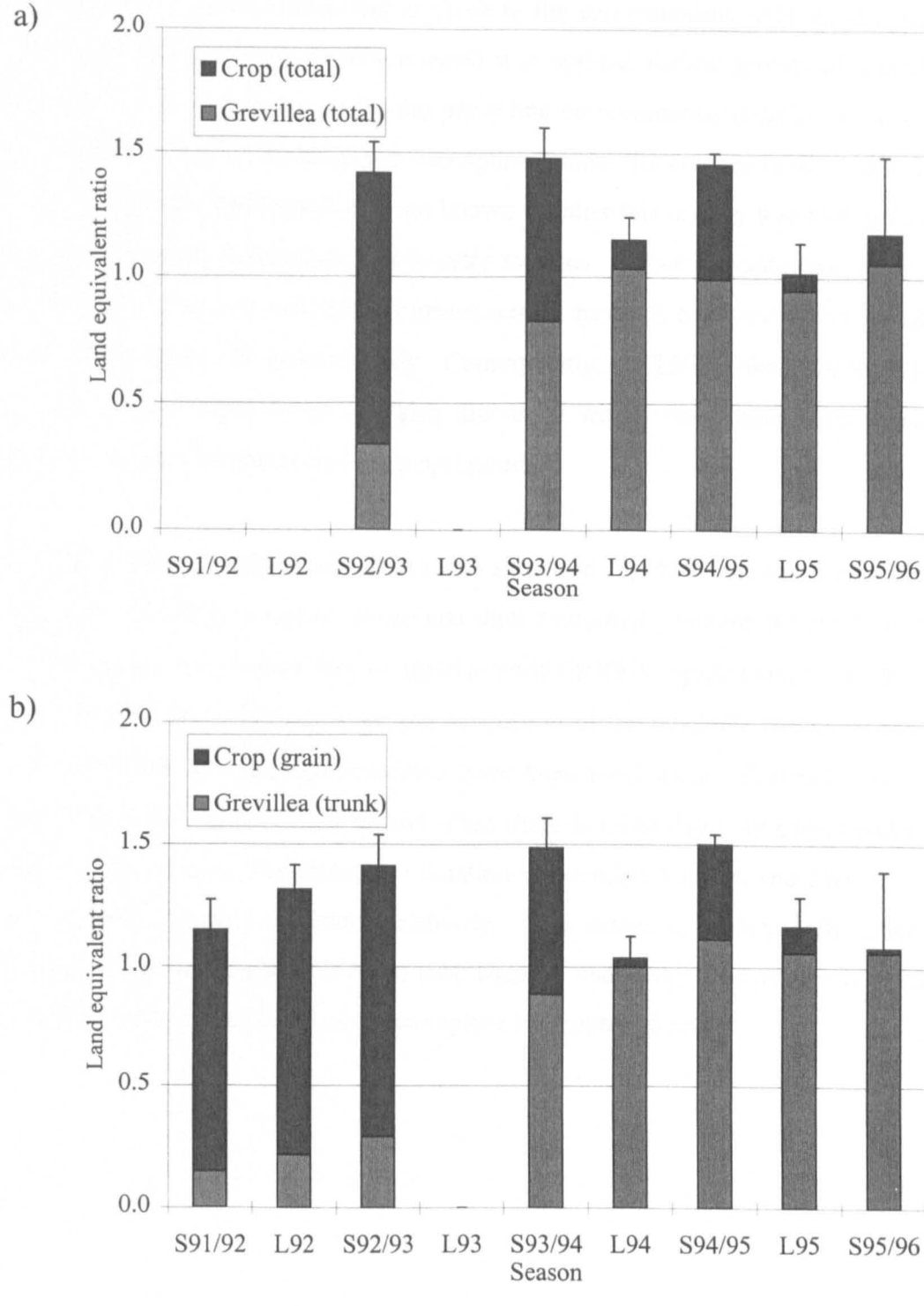


Figure 3.13 Seasonal land equivalent ratios (total column height) for the dispersed agroforestry (CTd) treatment calculated for a) total above ground biomass for both crop and grevillea and b) the main economic products; crop grain yield and grevillea trunk biomass. Single standard errors of the mean are shown.

were planted at densities identical to those in the corresponding sole stands, but it is unknown whether the tree density adopted was optimal for the growth of grevillea in either the Td or CTd stands under the prevailing environmental conditions. Likewise, although the density of the sole crop was optimal under the average local environmental conditions for the variety used, it is not known whether this density was also optimal for crop growth in grevillea-based agroforestry systems. However, optimisation of stand densities would require tremendous investment in research time and effort which was not available during the present study. Consequently, the LERs calculated for the CTd treatment may be either lower or higher than those which would have been obtained if the populations of all stands had been optimised.

The overall column heights and errors bars shown in Figure 3.13a and b represent the mean LERs for each cropping season and their associated standard errors of the mean; the LER values were greater than or equal to unity for all cropping seasons. LER values above one indicate either that a greater proportion of the available resources has been captured or that the captured resources have been used more effectively during the production of dry matter. This occurs when there is niche differentiation between the system components or, the green area duration is extended (Loomis and Connor, 1992), and provides evidence of complementarity. The extent to which each factor was responsible for ensuring that LERs at least equal to one in the CTd system is discussed in Chapter 7 after considering resource capture in Chapters 4 and 5.

CHAPTER 4

SHADING

The influence of microclimatic conditions in determining crop performance is well documented (Squire, 1990) and has been incorporated into a range of simulation models capable of predicting growth in a wide range of environments (e.g. Jones and Kiniry, 1986; Bradley and Crout, 1994). Similarly, the growth of trees within natural forest ecosystems or plantations and their impact on the wider environment is well understood (cf. Cannell, 1989; Friend *et al.*, 1997). However, the impact of trees on the microclimatic conditions experienced by associated crops and the question of whether interactions with trees alter their physiological responses relative to sole crops of the same species are less well understood (Ong *et al.*, 1996). Most previous studies of the influence of trees on the microclimatic conditions experienced by understorey crops have considered alley or hedgerow cropping systems (e.g. Corlett *et al.*, 1992; McIntyre *et al.*, 1996) or large trees grown as shelter belts (e.g. McNaughton, 1988; Brenner *et al.*, 1995); very few have considered the impact of dispersed overstorey tree arrangements (e.g. van den Beldt, 1990; Howard, 1997). At the outset of the CIRUS programme, it was anticipated that overstorey trees planted in a dispersed arrangement would modify the thermal environment and reduce incident radiation, atmospheric saturation deficit and water availability to understorey crops, but that the crop responses could be predicted using the principles established for equivalent sole crops. Modifications to the temperature and radiation environment are examined below, while the Institute of Hydrology is continuing to study saturation deficit and soil moisture.

4.1 IMPACT OF TREE CANOPY AND ARTIFICIAL SHADE ON THE CROP MICROCLIMATE

4.1.1 Temperature

Temperature is one of the major environmental factors affecting grain yield in maize (Muchow, 1990). Figure 4.1 shows the seasonal mean diurnal timecourses of

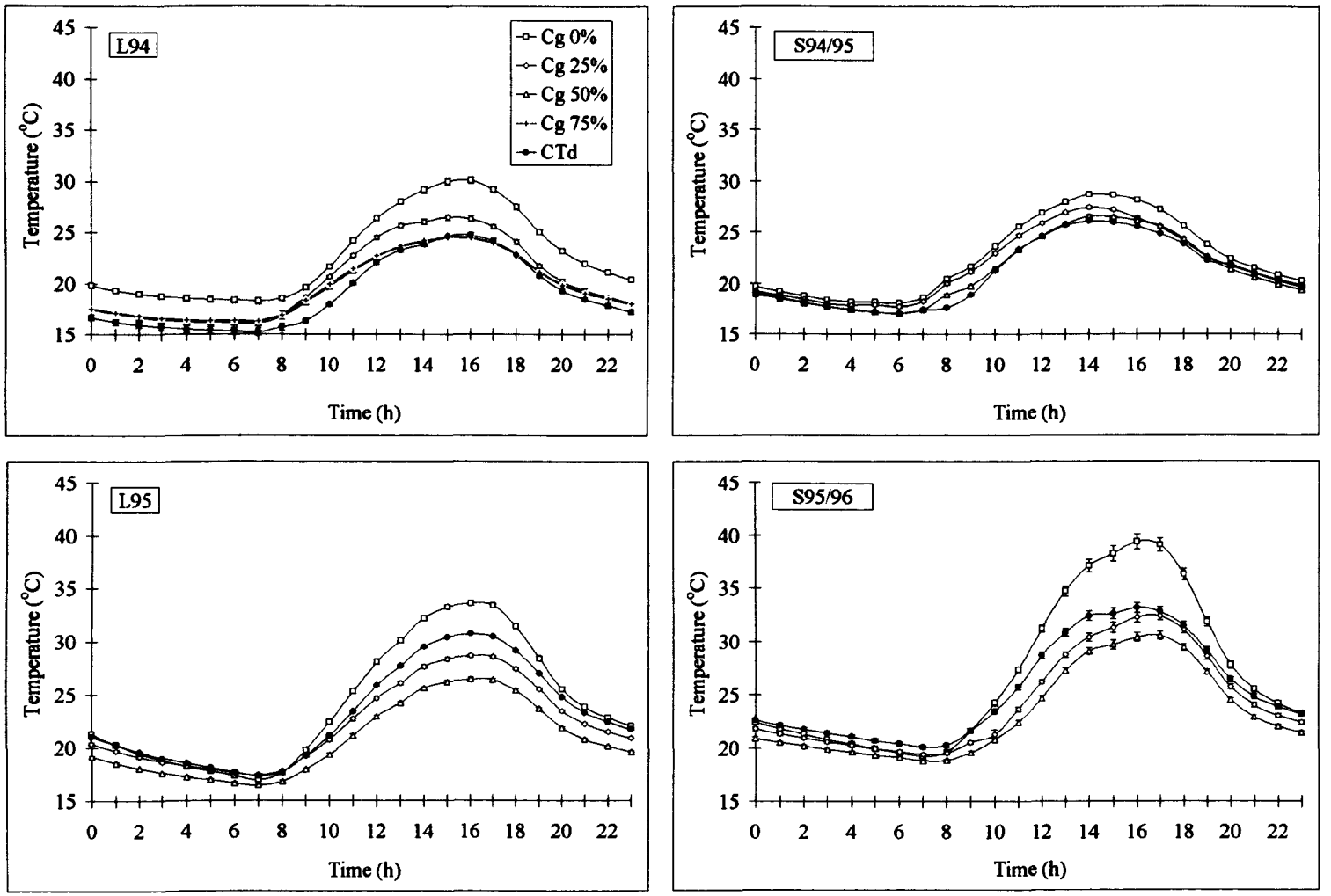


Figure 4.1 Seasonal mean diurnal timecourses of meristem temperature for maize grown under 0, 25, 50 and 75 % artificial shade or in the dispersed agroforestry treatment (CTd) during four seasons, L94 to S95/96. Double standard errors of the mean are shown except where these are smaller than the data symbols.

meristem temperature for maize grown as an unshaded sole crop or under natural and artificial shade during the four seasons between L94 and S95/96; each point is the mean of at least eight replicate measurements of meristem temperature located at the positions indicated in Figures 2.13, 2.14 and 2.15. Shade had a substantial moderating influence on meristem temperature. For example, the mean diurnal temperature range experienced by Cg 0% maize varied from 10 °C in S94/95 to 20 °C in S95/96, while the corresponding values for CTd maize ranged from 9 °C during L94 to 13 °C during L95; mean maximum meristem temperature was also reduced by up to 6 °C in CTd maize relative to unshaded sole maize. Similar substantial temperature modifications induced by the presence of a tree canopy were also reported by Ovalle and Avendano (1987), who recorded a 3-10 °C difference in maximum soil temperature in an *Acacia* woodland relative to the unshaded control. The mean diurnal timecourse for meristem temperatures under 25 and 50 % artificial shade were significantly higher than CTd maize during the first two seasons examined (L95 and S95/96; $p>0.05$), highlighting the substantial shading afforded by the tree canopy. However, the moderating influence of the tree canopy declined during the final two seasons (L95 and S95/96), with the result that mean meristem temperatures were significantly higher in CTd maize than in the shade net treatments ($p<0.001$). This decline in temperature moderation probably resulted from continued tree growth (cf. Section 3.1) and the progressive removal of the basal branches, which increased the distance between ground level and the base of the tree canopy to over 2 m, and thereby allowed greater throughflow of air to the understorey environment.

As stated previously (cf. Section 1.2.1), temperature may affect crop growth and development by affecting both the partitioning of photosynthate and the duration of the period of growth for individual organs (Squire, 1993). Super-optimal temperatures tend to be more detrimental to grain yield in maize than sub-optimal temperatures (Jones *et al.*, 1985; Rosenthal *et al.*, 1989). Shading may therefore be advantageous in semi-arid tropical environments where sole crops experience temperatures above the optimum for a significant proportion of their growth cycle. However, the benefits of shading will only be realised if the temperature moderation provided by tree shade creates a near optimal thermal environment for the understorey crop. Calculations of the number of hours during each season that the maize crops in CIRUS experienced

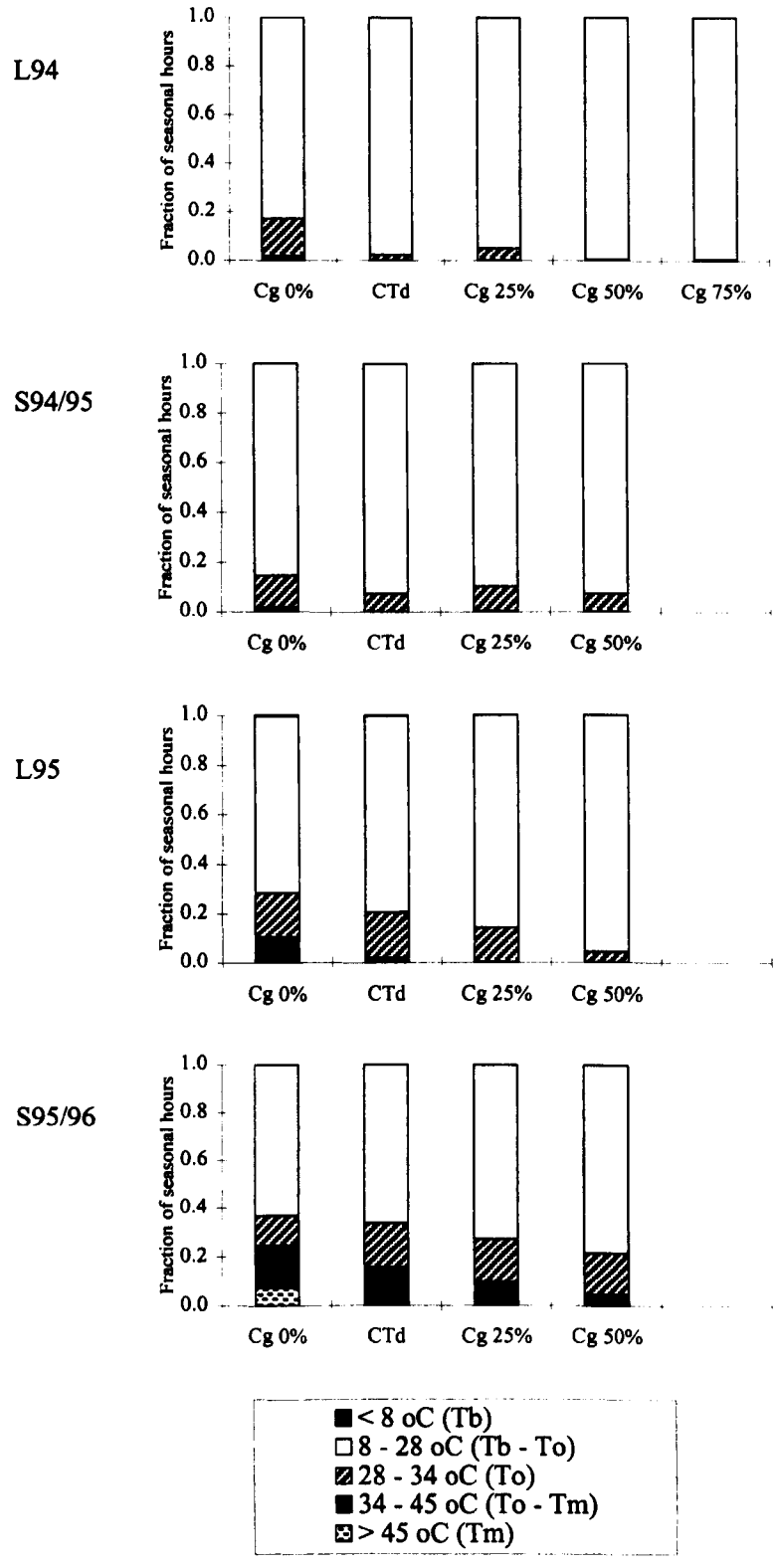


Figure 4.2 Fraction of seasonal hours corresponding to temperatures below the base temperature (<Tb) and above the maximum temperature (>45), and within the range of sub-optimal (Tb -To), optimal (To) and super-optimal (To - Tm) temperatures as experienced by maize meristems during each of the cropping seasons examined.

near-optimal, sub-optimal and super-optimal temperatures for growth enabled the relative impact of shading on the thermal environment to be quantified (Fig. 4.2). No apparent advantage of shading was observed during the L94 or S94/95 short growing seasons since the number of hours at near-optimum temperatures was greatest in the unshaded Cg 0% maize and the incidence of super-optimal temperatures was minimal. However, the thermal environment was most favourable for maize growth in the CTd treatment during the L95 season and in the Cg 50% shade treatment in S95/96.

The moderation of understorey temperature seen in CIRUS is not necessarily applicable to all agroforestry systems. For example, in Niger, Brenner *et al.* (1995) attributed the poor growth and yield of millet in the lee of windbreaks, relative to unsheltered control crops, to increases in both soil surface and leaf temperatures. Although the present study differed from that of Brenner *et al.* (1995) in several respects, not least in its denser arrangement of trees within the cropping area, this comparison highlights the difficulty of predicting the effects of shade provided by trees on understorey temperature under different environmental conditions. Bhatt *et al.* (1991) attempted to characterise the suitability of trees for semi-arid agroforestry systems by determining the exchange of energy from their canopies. Canopies that lost most energy by radiative transfer and transpiration, and thereby experienced a negative flow of convective energy, were considered to indicate tree species capable of surviving in environments where air temperatures were high. These species might prove beneficial to understorey crops by reducing the thermal load imposed on them and therefore enhance their rates of growth and development. In addition, modifications to soil temperatures might have important implications for seedling survival, soil water status, and possibly the rate of litter breakdown and N-mineralisation (Ludlow and Muchow, 1990). Further studies to identify suitable agroforestry tree species for temperature moderation under dryland conditions are clearly required, although it must be recognised that there is inherent risk in defining suitability on the basis of a single microclimatic factor.

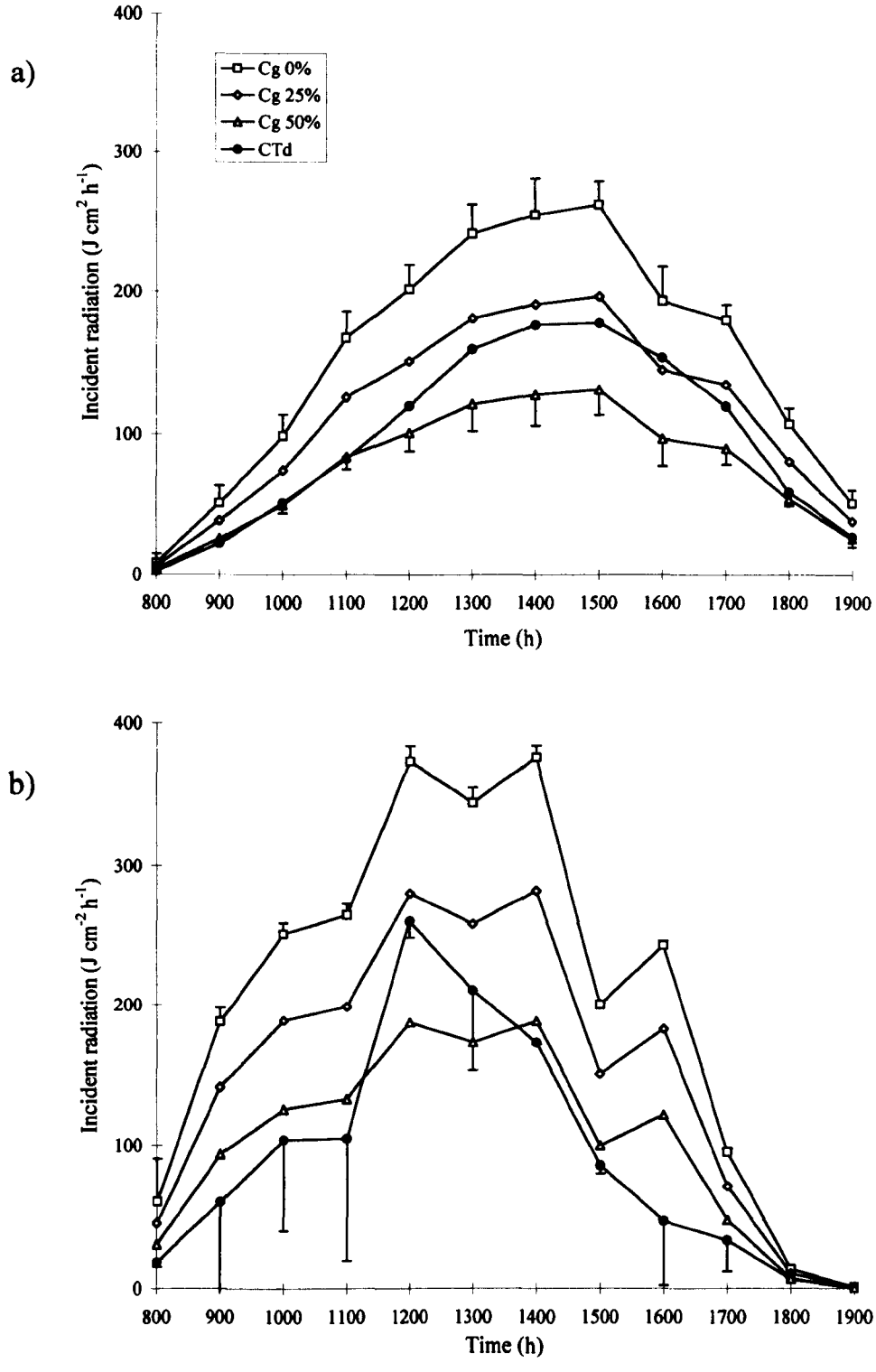


Figure 4.3 Mean diurnal timecourses of short-wave radiation incident upon maize in the Cg 0%, Cg 25%, Cg 50% and CTd treatments during an 11 day period centred around anthesis during a) S94/95 and b) S95/96 seasons. Single standard errors of the mean are shown for Cg 0% and CTd treatments only.

4.1.2 Solar radiation

Figure 4.3 shows mean diurnal timecourses for total short-wave radiation incident upon maize in the Cg 0%, Cg 25%, Cg 50% and CTd treatments over an 11 day period centred around anthesis during the S94/95 and S95/96 seasons. Incident radiation decreased as shading intensity increased in the shade net treatments, while the values for CTd maize were intermediate between the Cg 25% and Cg 50% treatments. The values for CTd maize are means calculated on the assumption that shading was uniform throughout the cell bounded by four neighbouring trees. However, in reality the discontinuous nature of the tree canopy caused substantial local variation in shading intensity depending on proximity to the trees and solar angle. This is illustrated by the large standard errors associated with the CTd measurements during S95/96, (Fig. 4.3) and the shading patterns shown in Plate 2.10 and Figure 4.5. Maximum incident radiation values were lower during S94/95 than S95/96, which are probably a consequence of the more overcast skies associated with the unusually high rainfall received during the former season. Mean daily incident radiation calculated over the same period shown in Figure 4.3 also highlights the greater incident radiation experienced during S95/96 compared to S94/95. However, the mean daily incident radiation for CTd maize was slightly higher in S94/95 than in S95/96 (1153 *vs.* 1106 J cm^{-2} d^{-1}), reflecting the increased shade provided by the larger tree canopy (Fig. 3.1b).

Hourly short wave solar radiation measurements were used to calculate cumulative interception for each treatment during S94/95 (Fig. 4.4). Incident radiation frequently exceeded 20 MJ m^{-2} d^{-1} (cf. Fig. 2.1) and the cumulative incident radiation during the 123 day season was 2432 MJ m^{-2}. The sole tree and crop canopies respectively intercepted 720 and 630 MJ m^{-2}, while the combined tree and crop canopies in the CTd treatment accumulated 950 MJ m^{-2}, 33 and 50 % more than in the sole tree and crop treatments respectively.

Figure 4.5 shows the spatial variation in total seasonal radiation incident on the understorey maize growing in four adjacent cells of the CTd treatment during the S94/95 season. This figure is comparable to Figures 3.8 and 3.9, which illustrate the

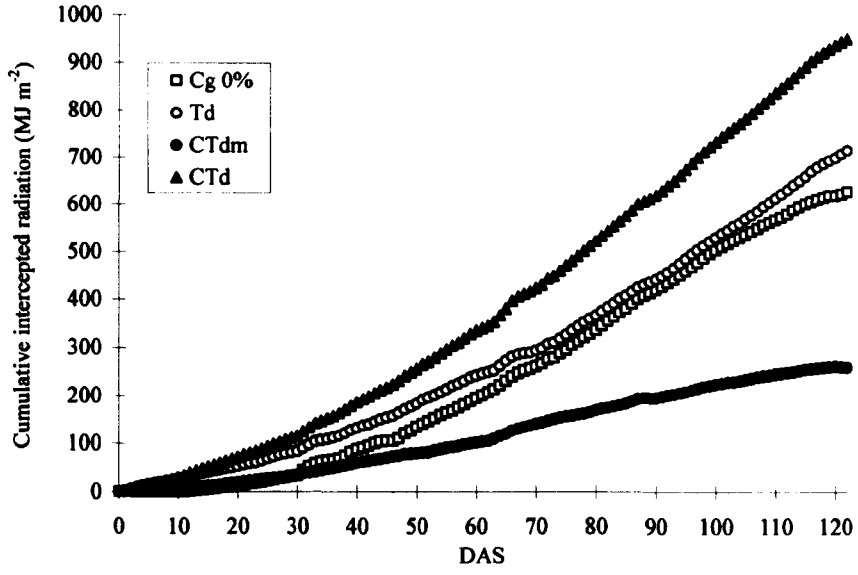


Figure 4.4 Cumulative intercepted radiation by sole maize (Cg 0%) and sole grevillea (Td) canopies, the maize canopy estimated independently of grevillea in the dispersed agroforestry treatment (CTdm) and the combined grevillea and maize canopies in the agroforestry treatment (CTd) during the S94/95 season.

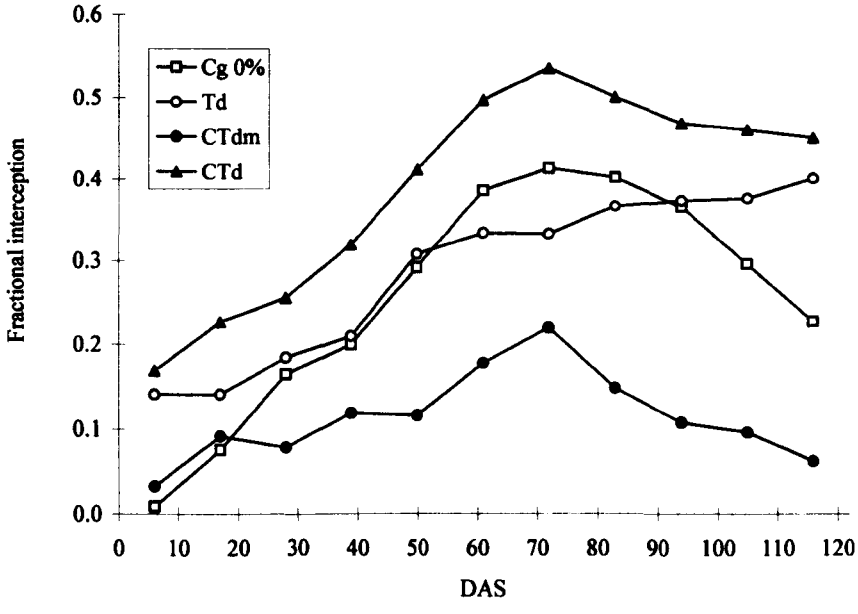


Figure 4.6 Fractional interception by sole maize (Cg 0%) and sole grevillea (Td) canopies, the maize canopy estimated independently of grevillea in the dispersed agroforestry treatment (CTdm) and the combined grevillea and maize canopies in the agroforestry treatment (CTd) during the S94/95 season.

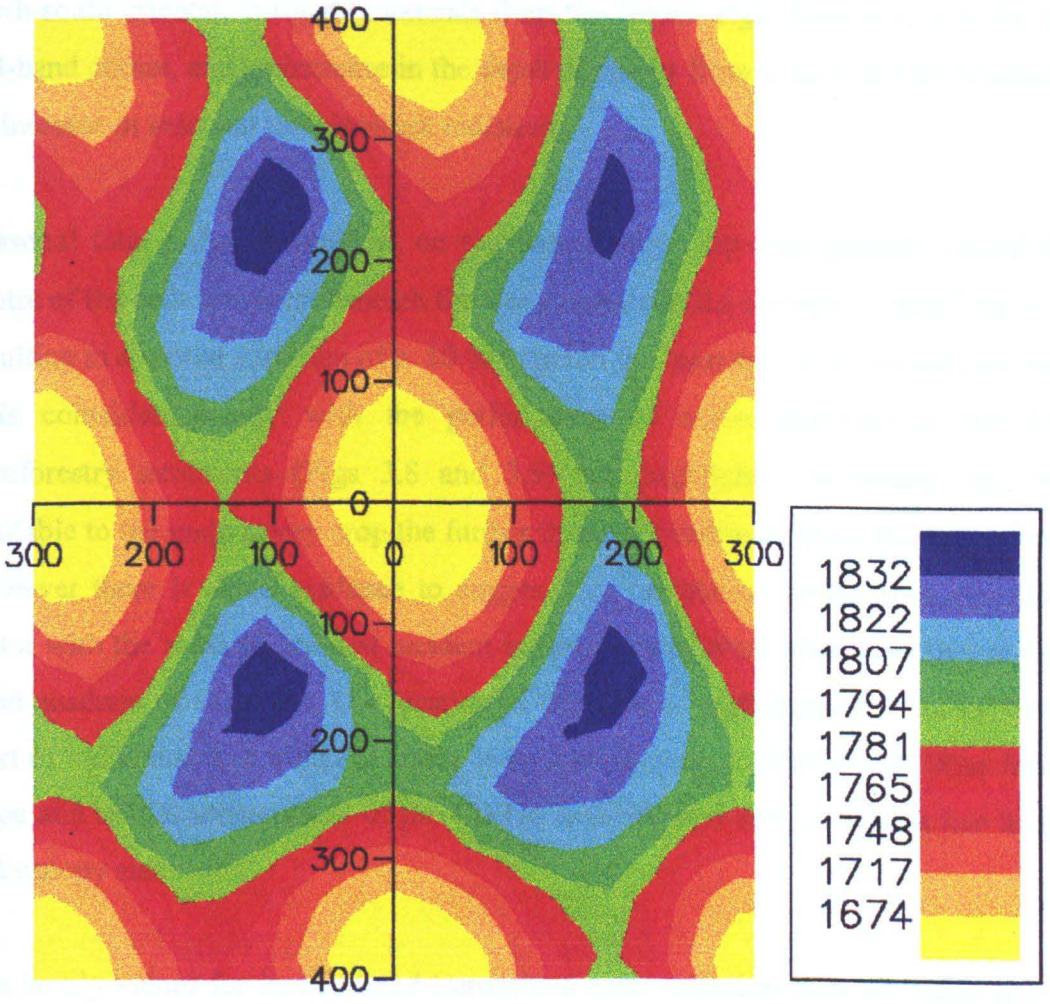


Figure 4.5 Spatial variation of mean seasonal total radiation (MJ m^{-2}) incident on the understorey maize for four adjacent cells in the dispersed agroforestry treatment (cf. Figure 2.14) during the 1994/95 short growing season. The axes indicate distance (cm) from the central tree of four cells.

performance of maize growing at different distances and orientations relative to the nearest tree. It is important to note that for consistency with Figures 3.8 and 3.9, the same interpolation and plotting procedures have been adopted for Figure 4.5, the north-south orientation roughly extends from the bottom right-hand corner to the top left-hand corner, and an increase in the depth of colour from yellow to blue illustrates an increase in seasonal total incident radiation.

Seasonal total radiation incident on the understorey crop was greatest toward the centre of the cells and least beneath the tree canopies at the corners of cells (Fig. 4.5), resulting in a spatial variation of c. 10 % between the least and most shaded position. This coincides exactly with the performance of maize growing in the CTd agroforestry treatments (Figs 3.8 and 3.9) and highlights the greater resources available to the understorey crop the further they are positioned from the nearest tree. However there is some evidence to suggest that orientation could be a significant factor with the areas of greatest incident radiation being skewed toward the top right hand quadrant of each cell. The location of this area of high incident radiation to the west of individual tree trunks is likely to be a consequence of the South West facing slope and spatial arrangement of the CIRUS experimental site, as well as tree height and canopy size.

The hourly values for incident and transmitted solar radiation over the entire season were used to calculate daily mean values for fractional intercepted radiation (f)using:

$$f = 1 - \left(\frac{S_t}{S}\right) \qquad \text{Equation 4.1}$$

where S denotes total daily incident solar radiation recorded by the reference solarimeters (cf. Section 2.7.1) and S_t is the daily total transmitted radiation beneath the tree, crop or combined tree and crop canopies. The ground-level measurements of solar radiation in the dispersed agroforestry treatment (CTd) provided values for the combined interception by the maize and grevillea canopies. In order to calculate interception by maize, estimates of interception by the grevillea canopy and hence the quantity of light reaching the understorey crop canopy were required. However, the

restricted number of solarimeters and logger channels available precluded direct measurement of interception by the tree canopy in the CTd treatment, making it necessary to infer values from measurements made in the sole tree treatment (Td). This was achieved by calculating a correction factor (p) to account for differences between these treatments in shading pattern, the installation heights of the solarimeters (cf. Section 2.7.1), and consequent differences in radiation levels resulting from height differences between the solarimeters and the base of the tree canopy. This correction factor is the slope of the linear correlation passing through the origin between the mean values recorded in the CTd and Td treatments before crop emergence and after crop harvest and is calculated independently for each season. For S94/95 the p value was 1.0284 with an r^2 value associated with the linear regression of 0.94. The correction factor was then applied as follows:

$$S_{t(CTdt)} = \frac{S_{t(Td)}}{p} \qquad \text{Equation 4.2}$$

$$S_{t(CTdm)} = S_{t(CTd)} - \frac{S_{t(Td)}}{p} \qquad \text{Equation 4.3}$$

where $S_{t(CTdt)}$, $S_{t(Td)}$, $S_{t(CTdm)}$ and $S_{t(CTd)}$ respectively represent transmitted radiation beneath the CTd grevillea, Td grevillea, CTd understorey maize, and the combined grevillea and maize canopies in the CTd treatment.

Figure 4.6 illustrates the seasonal timecourses for fractional interception of shortwave radiation during S94/95. The sole maize (Cg) canopy developed rapidly, and f reached a maximum of c. 0.40 around the time of flowering, close to the time of maximum LAI (Fig. 3.7); this value was maintained for c. 30 d prior to the onset of rapid senescence. The f values for the sole tree canopy exhibited an initial lag period before responding to the high seasonal rainfall by increasing rapidly between 20-50 DAS to c. 0.33; this rapid expansion coincided with the substantial increase in LAI during the same period shown in Figure 3.1b. Thereafter, the f values for the Td treatment increased steadily to a maximum of 0.40 as the canopy expanded. Fractional interception by the combined tree and crop canopies in the CTd treatment was consistently greater than in the sole tree and crop treatments, reaching a

maximum of 0.54 and following a timecourse similar to that for Cg maize, although the decline in *f* was less pronounced during the final 30 DAS. Since fractional interception by the understorey maize canopy (CTdm) was calculated from the difference in interception between the CTd and Td systems (Eq. 4.3), the *f* values for this component will be influenced by any difference between these treatments in the growth rate of the tree canopies. The growth response of the tree canopies to the prevailing favourable soil moisture conditions between 20-50 DAS differed between the Td and CTd treatments, probably due to competition for water between the CTd trees and the understorey maize. As a consequence, the *f* values for the CTdm canopy apparently decreased during two measurement intervals (17-28 and 39-50 DAS). This is likely to have been an artefact of the method used to calculate interception by the CTdm maize.

Seasonal mean *f* values may be calculated from mean daily values recorded between sowing and final harvest. Squire (1990) compared seasonal *f* values from the literature for various field crops grown under well watered and fertilised conditions and concluded that the values for short duration cereals are typically in the region of 0.5. However, since *f* depends on canopy architecture and the phenology of the vegetation involved, any factor, which reduces growth and development or alters canopy structure may affect *f*. Seasonal mean *f* values for maize and grevillea during S94/95 are shown for all treatments in Table 4.1. Even during this season of relatively high rainfall (628 mm *vs.* long-term average of 350 mm), the *f* value for sole maize of 0.26 was approximately half that cited by Squire (1990), suggesting that canopy size was limited by a lack of water or nutrients, or by the population density. Mean seasonal fractional interception by the combined tree and crop canopies in the CTd treatment (0.39) was c. 50 % greater than that for Cg maize, suggesting the existence of substantial spatial complementarity. This finding confirms suggestions by Keating and Carberry (1993) and Ong *et al.* (1996) that spatial complementarity occurs only when the *f* values for sole stands are sub-optimal, and indicates that the productivity of the agroforestry system examined was potentially greater than either of the sole systems during the dry season.

Table 4.1 Total seasonal intercepted radiation, mean fractional interception (*f*), total above-ground biomass at harvest, seasonal mean radiation conversion coefficient (*e*) and *e* calculated between planting and flowering for maize and grevillea during the S94/95 growing season.

Treatment	Intercepted radiation ($MJ\ m^{-2}$)	Seasonal *f*	Biomass ($T\ ha^{-1}$)	*e* ($g\ MJ^{-1}$)	*e* up until flowering ($g\ MJ^{-1}$)
Cg 0%	630	0.26	3.28	0.52	1.04
Td	718	0.29	5.07	0.71	-
CTd	952	0.39	6.65	0.70	-
CTdm	261	0.11	1.64	0.63	0.88

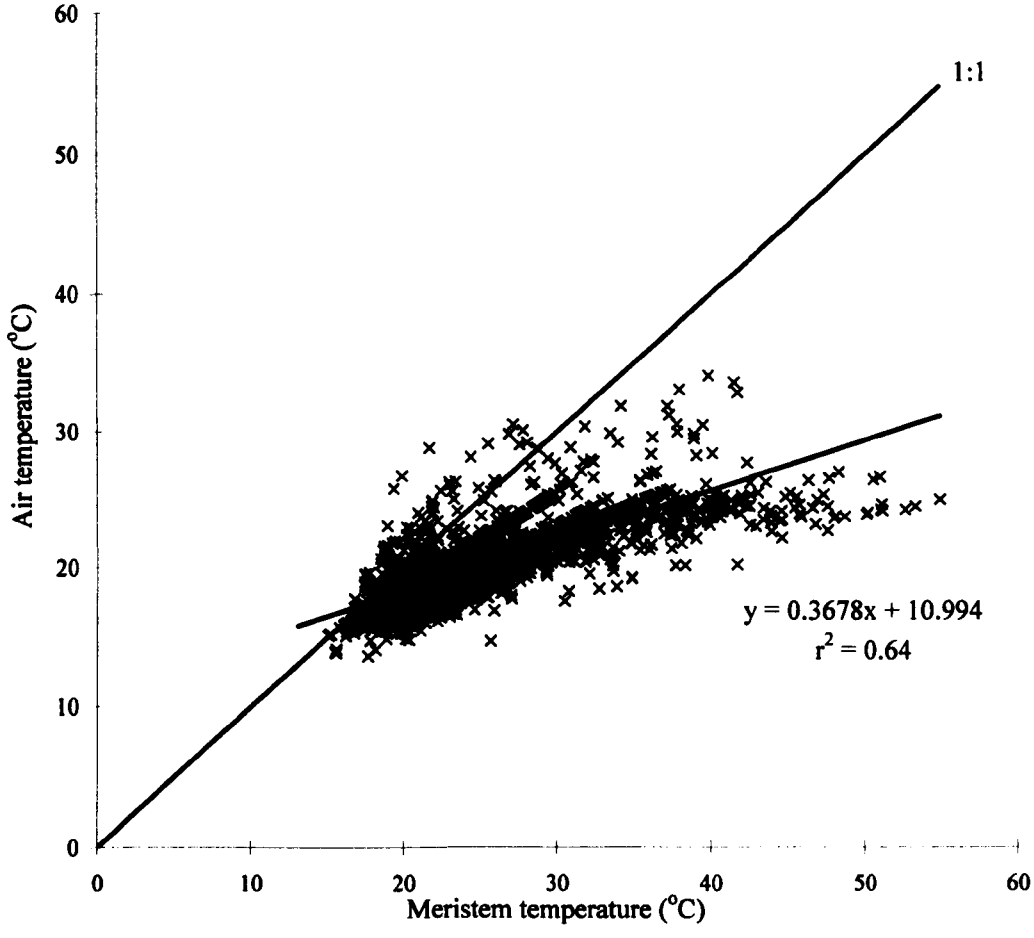


Figure 4.7 Correlation between meristem temperature in maize and air temperature in CIRUS. The data represent hourly values recorded during all four experimental seasons (L94-S95/96)

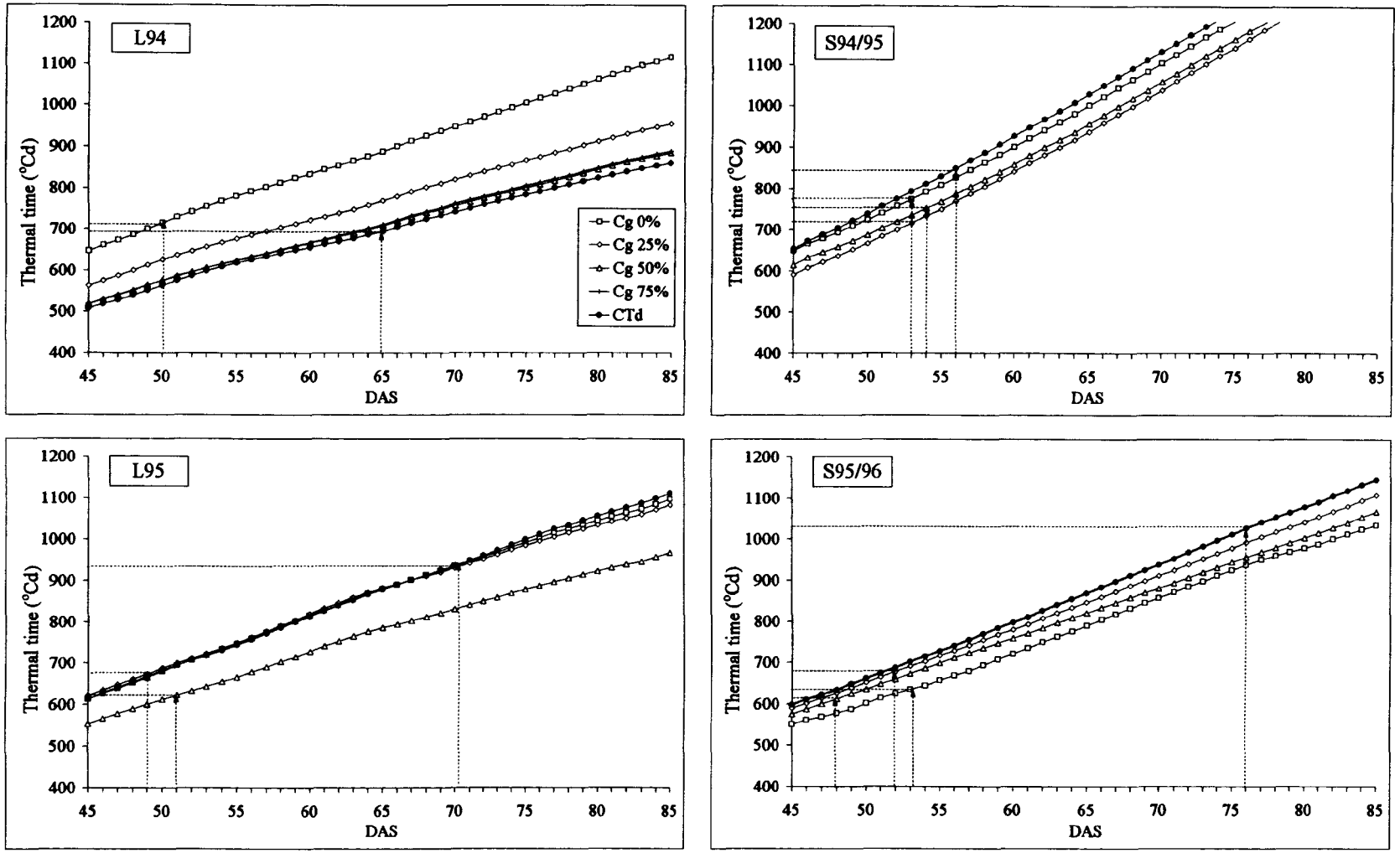


Figure 4.8 Relationship between the accumulation of thermal time and days after sowing (DAS) for maize grown under 0, 25, 50 or 75 % artificial shade (Cg 0%, Cg 25%, Cg 50% and Cg 75% respectively) or in the dispersed agroforestry treatment (CTd) during four seasons, L94 to S95/96. Arrows indicate the length of time between sowing and flowering measured in days and the associated thermal duration.

4.2 RESPONSE OF MAIZE TO SHADING BY THE GREVILLEA CANOPY AND ARTIFICIAL SHADE NETS

4.2.1 Temperature effects and thermal time

Many studies of the influence of thermal time on developmental processes have depended on measurements of daily mean air temperature (e.g. Lenga and Keating, 1990) or maximum and minimum temperatures (Lyamchai *et al.*, 1997) for the calculation of thermal time. These are often the only values available from field experiments, but may not be the most appropriate for thermal time calculations since the rate of developmental processes depends more closely on meristem than air temperature, and responds on much shorter timescales than can be captured by daily temperature measurements. The reliability of thermal time calculations should therefore be greatly improved by the approach adopted in the current study of measuring meristem temperature in maize at five minute intervals between emergence and maturity. Gallagher (1979) observed little difference between soil (at 2 cm depth) and air temperatures in the field, indicating that meristem temperature in cereals may be estimated accurately from air temperature even before the meristem emerges above ground-level. In contrast, comparison of the measurements of air temperature with estimated meristem temperature (cf. Section 2.7.2) during the first experimental season (L94; Fig. 4.7) demonstrated the existence of substantial differences.

The long-term impact of the temperature amelioration on the shaded crop may be illustrated by determining the relationship between accumulated thermal time and the timing of key developmental events. Figure 4.8 shows the accumulation of thermal time in maize during all four experimental seasons between L94 and S95/96; each point is the mean of at least eight replicate measurements of meristem temperature. The slope of the lines for each treatment represents the rate of thermal time accumulation, while the arrows indicate the mean time of flowering (DAS) for each treatment and the associated thermal duration (degree days) where there is a discernible difference between treatments. Thermal time accumulated more rapidly in all treatments during S94/95 than in any other season since temperatures were consistently closer to the optimum.

As temperature is the primary determinant of development in maize in the absence of stress, the thermal duration of specific developmental stages would be expected to be comparable in plants exposed to differing thermal environments under otherwise comparable conditions. The considerable variation between treatments and seasons in the quantity of thermal time required to reach flowering (Fig. 4.8) clearly demonstrates that development was affected by factors other than temperature (Corlett, 1989), although the precise nature of these effects could not be established from the data available. Flowering was generally later in CTd than in Cg 0% maize when expressed in both chronological and thermal time, by up to 24 days and 400 °Cd during S95/96; the thermal time required to flowering increased in the CTd maize as the trees grew larger. The differences between the Cg 0%, Cg 25% and Cg 50% shade net treatments were much smaller, amounting to no more than five days or 80 °Cd. The differing responses observed under natural and artificial shade suggest that the substantial delay in flowering in CTd maize resulted from below-ground competition with grevillea for water and nutrients. Siemer *et al.* (1969) has previously identified moisture deficiency as being capable of significantly delaying development in maize. Thus, the potentially beneficial effect of shading on crop temperatures in areas such as Rajasthan, where very high mid-day soil temperatures (45-55 °C; Khalifa and Ong, 1990) are experienced, may not be fully realised. This is because suppression of growth and development by below-ground competition may negate any advantage provided by the more favourable thermal environment.

4.2.2 Photosynthesis, transpiration and radiation conversion coefficients

Figures 4.9 and 4.10 illustrate the impact of artificial shade and the presence of overstorey trees on net photosynthetic and transpiration rates (Pn and Et) for sole and intercropped maize during the unusually wet (628 mm) 1994/95 short growing season (S94/95; Fig. 4.9) and the much drier (302 mm) 1995 long growing season (L95; Fig. 4.10). The measurements were made using four plants per treatment beginning at 0930, 1130, 1400 and 1630 h local time at 7-10 d intervals between 30-100 DAS during each season. Pn, Et and incident radiation values for the CTd treatment were expressed as treatment level means. Incident PAR declined as shading intensity increased in the shade net treatments and also decreased progressively for CTd maize

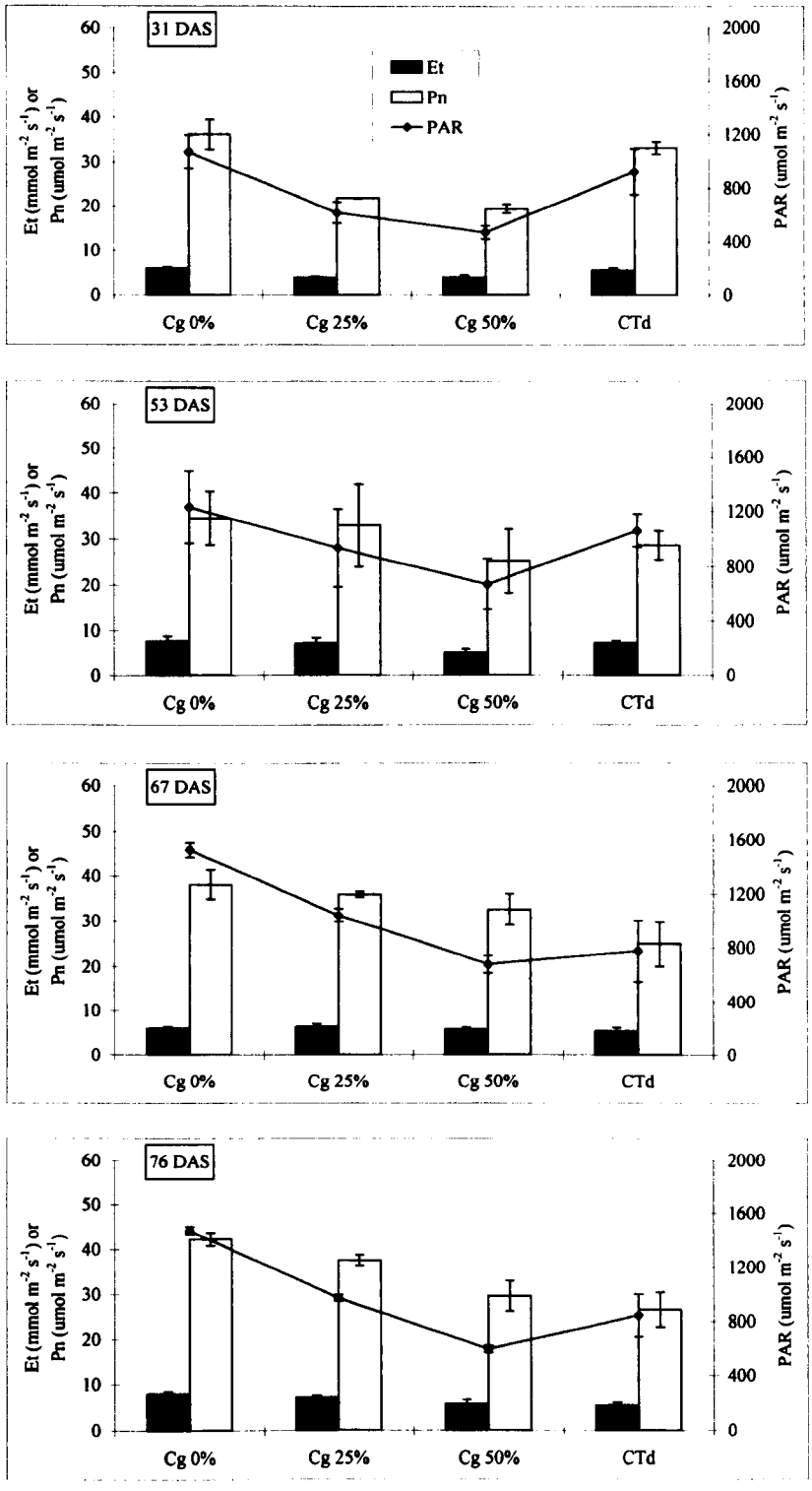


Figure 4.9 Photosynthetic (Pn) and transpiration (Et) rates and incident PAR fluxes for maize grown under 0, 25 and 50 % artificial shade (Cg 0%, Cg 25% and Cg 50%) and in the dispersed agroforestry treatment (CTd) during the 1994/95 short growing season. The data represent the diurnal means for four plants measured at c. 0930, 1130, 1400 and 1630 local time. Double standard errors of the mean are shown.

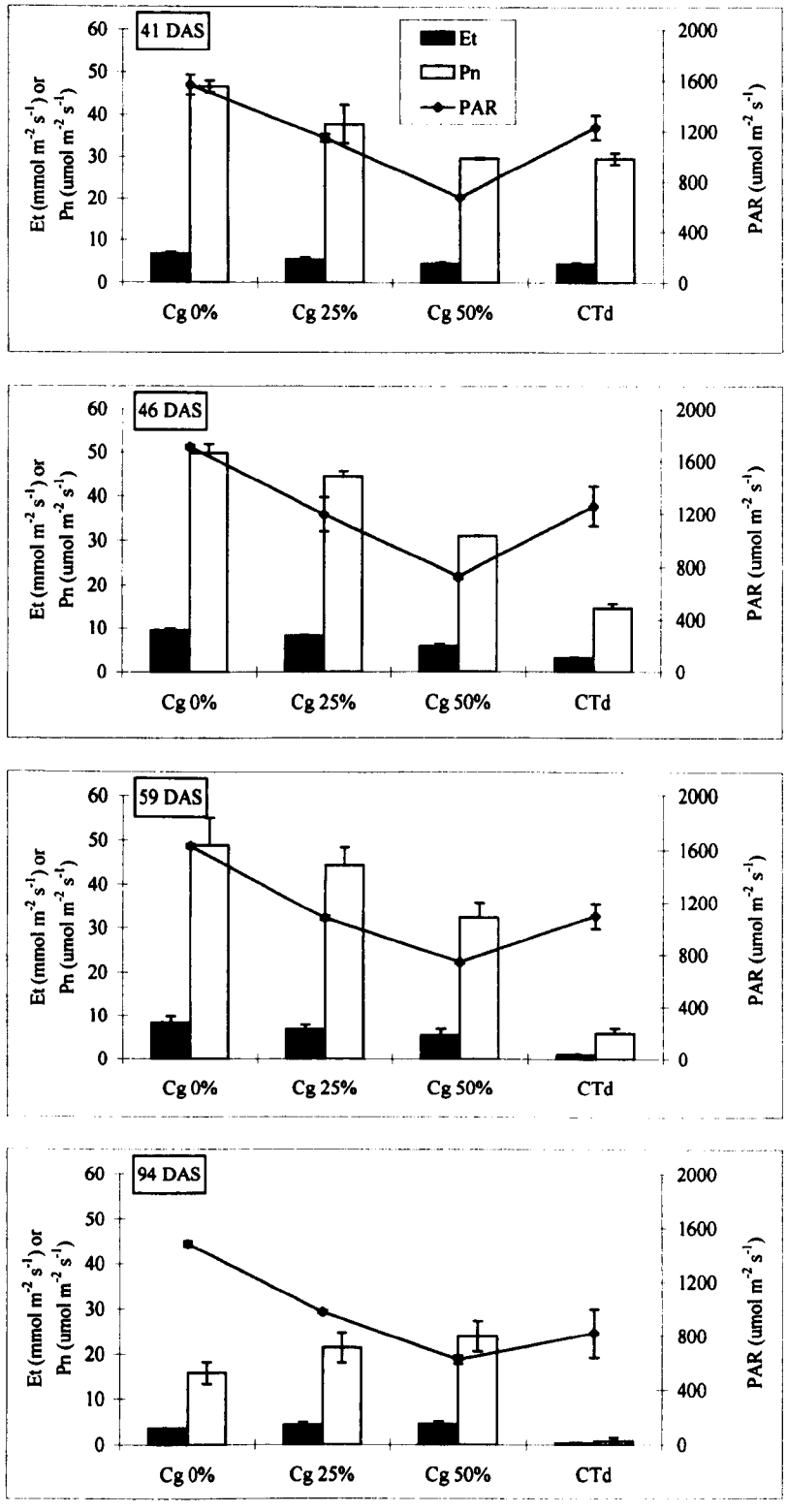


Figure 4.10 Photosynthetic (Pn) and transpiration (Et) rates and incident PAR fluxes for maize grown under 0, 25 and 50 % artificial shade (Cg 0%, Cg 25% and Cg 50%) and in the dispersed agroforestry treatment (CTd) during the 1995 long growing season. The data represent the diurnal means for four plants measured at c. 0930, 1130, 1400 and 1630 local time. Double standard errors of the mean are shown.

as the tree canopy increased in size during both seasons. The presence of the trees hardly affected Pn and Et in the CTd treatment during the early part of the wet S94/95 season (Fig. 4.9). However, both parameters declined relative to unshaded sole maize (Cg 0%) as the season progressed, although neither declined below 60 % of the corresponding Cg 0% values. This pattern reflects the timecourses for leaf area (Fig. 3.7) and fractional interception (Fig. 4.6) in CTd maize, which were similar to those for sole maize during the early stages of the season but subsequently declined. Pn and Et in CTd maize declined sharply during L95 (Fig. 4.10) from values similar to those for the Cg 25% and Cg 50% shade net treatments at 41 DAS to c. 10 % of the Cg 0% treatment at 94 DAS.

The view that water availability was the dominant factor influencing the productivity of understorey maize is supported by a comparison of the responses of CTd maize with those of sole maize grown under nets to provide shade while avoiding below-ground competition. The values for CTd maize were similar to those for the Cg 25% and Cg 50% treatments during the wet S94/95 season (Fig. 4.9), in agreement with the mean seasonal reduction in incident radiation of c. 30 % provided by the tree canopy. However, the reductions in Pn and Et in CTd maize during the drier L95 season were much greater than those induced by artificial shade, suggesting that competition for water was the primary factor limiting the productivity of understorey maize.

Figure 4.11 illustrates the mean diurnal timecourses for incident PAR, Pn and Et and stomatal conductance in the CTd, Cg 0%, Cg 25% and Cg 50% treatments at anthesis in the sole maize treatments (55 DAS) in S95/96. As expected, incident PAR was consistently greatest in the Cg 0% treatment ($p<0.05$) and the values for both physiological variables tracked the diurnal timecourse for incident PAR in all treatments. The mean diurnal timecourses for each physiological variable in CTd maize were consistently lower than in the sole maize treatments ($p<0.05$).

The photosynthetic light response curves (Fig. 4.12) were similar in all the various sole maize treatments irrespective of shading intensity, although the light-saturated value for Pn was slightly lower in the Cg 50% treatment than in the Cg 0% and Cg 25% treatments at 25 and 45 DAS. By 85 DAS, the maize was c. 30 days into the

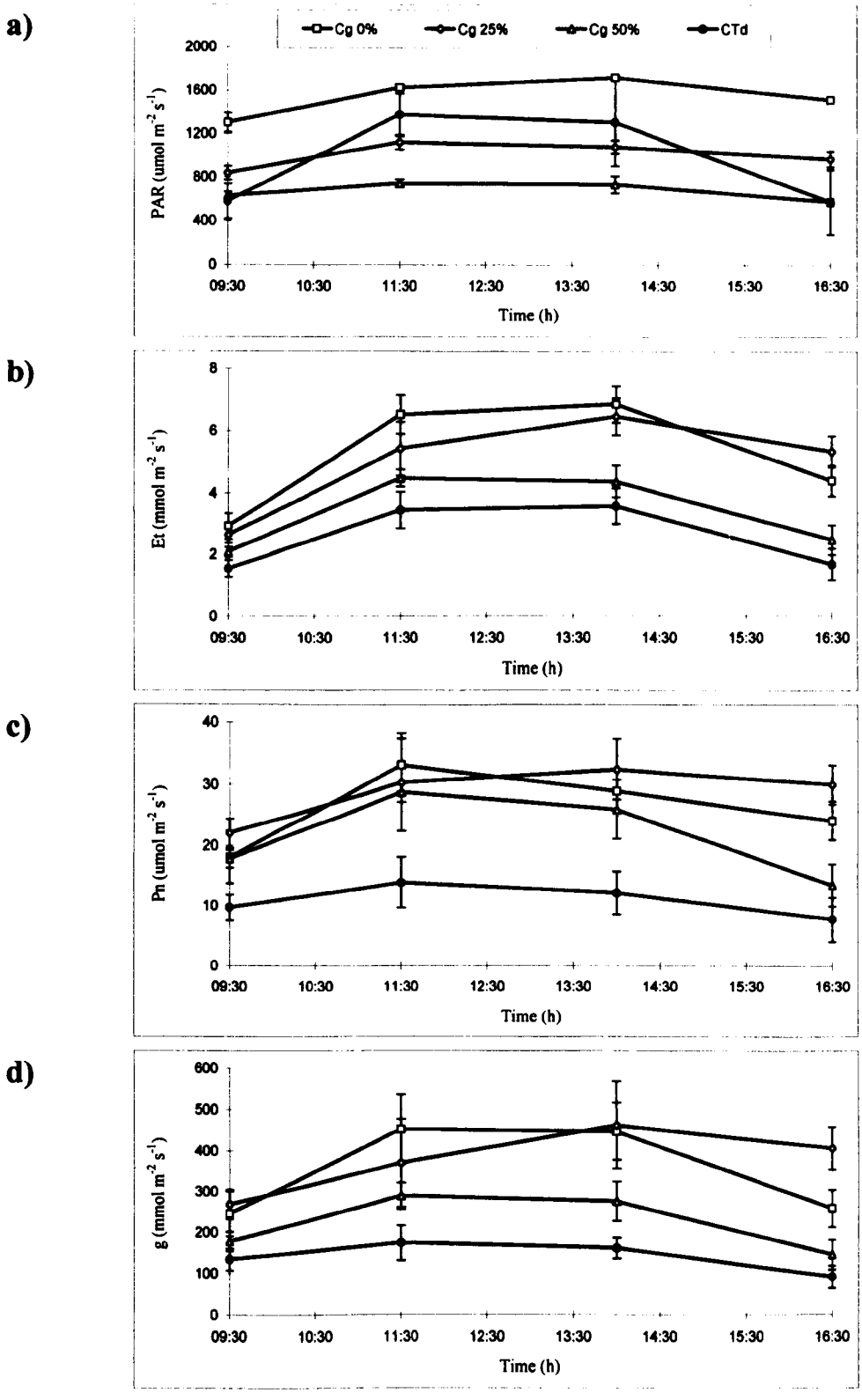


Figure 4.11 Diurnal timecourses for: a) incident PAR, b) transpiration rate, c) photosynthetic rate, and d) stomatal conductance. Data are shown for maize grown under 0, 25 and 50 % artificial shade (Cg 0%, Cg 25% and Cg 50%) and in the dispersed agroforestry treatment (CTd) for one day (55 DAS) during the 1995/96 short growing season. The data represent the means for four plants. Double standard errors of the mean are shown.

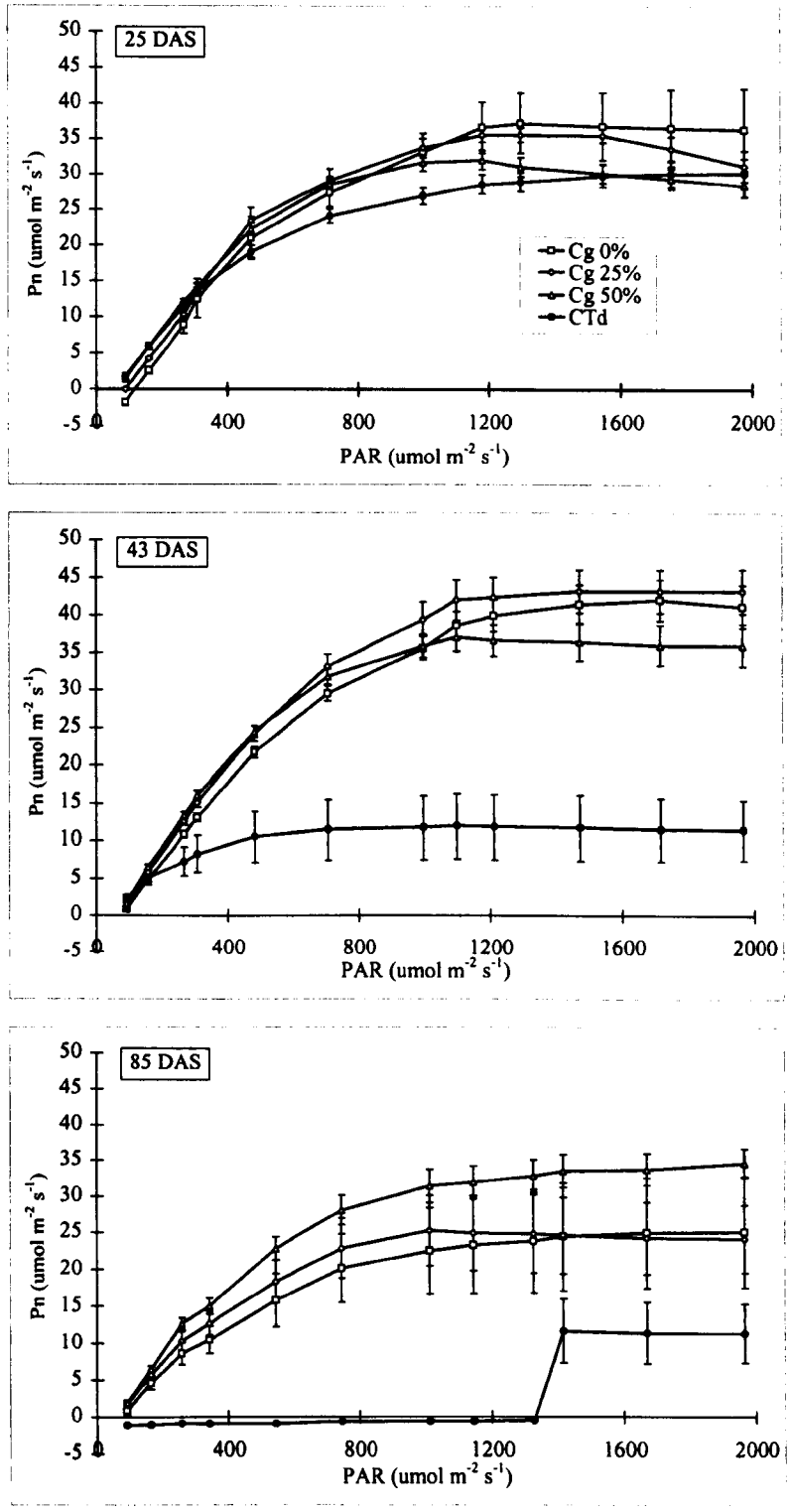


Figure 4.12 Light response curves for net photosynthesis (Pn) in maize on three occasions (25, 43 and 85 DAS) during the 1995/96 short growing season. The data represent the mean response of four plants in each treatment. Double standard errors of the mean are shown.

grain filling period and approaching maturity in all treatments. The onset of senescence reduced photosynthetic competence in all treatments, as illustrated by the c. 40 % reduction in light-saturated Pn in the Cg 0% and Cg 25% treatments between 43 and 85 DAS. However, the light-saturated Pn value for the Cg 50% treatment at 85 DAS was similar to that at 43 DAS, suggesting that senescence was delayed by the lower temperatures and higher soil water status experienced within this treatment. The sharp step in the CTd curve at c. 1350 mmol m^{-2} s^{-1} PAR at 85 DAS may reflect the severely limited water availability at this time, which may have triggered rapid stomatal closure and the complete cessation of Pn during measurements.

Light-saturated Pn was drastically reduced relative to sole maize after c. 43 DAS at all locations in CTd maize (Fig. 4.12). Shading by the trees decreased seasonal total shortwave radiation incident upon CTd maize by c. 25-35 % during the 1995/96 short growing season. Thus if the photosynthetic capacity of CTd maize had been affected only by the intensity of shade provided by the tree canopy, its photosynthetic response curve would have been intermediate between those for the Cg 25% and Cg 50% shade net treatments. However, the maximum Pn value at light saturation for CTd maize of 12 mmol m^{-2} s^{-1} was less than one third of that for sole maize, and occurred at a PAR flux of c. 500 as opposed to c. 1100 umol m^{-2} s^{-1}. These results clearly indicate that the growth potential of the CTd maize was limited not only by reductions in incident PAR but also by decreased photosynthetic competence. This is reflected by the virtual failure of CTd maize during this season (Fig. 3.6).

The radiation conversion coefficient (*e*) is essentially determined by the balance between the rates of photosynthesis and respiration (Monteith 1981), and may be considered either in relation to light response curves for photosynthesis for the whole canopy or individual leaves, or determined empirically from the relationship between above-ground biomass and the quantity of solar radiation intercepted (Ludlow and Muchow, 1990). As light availability is the key determinant of photosynthetic efficiency at PAR fluxes below c. 200 umoles m^{-2} s^{-1}, the slope of the tangent to the photosynthesis curve in this region may be assumed to provide a measure of the radiation conversion coefficient (*e*). The values for maize did not differ significantly between treatments in S95/96, although *e* was consistently lower in the CTd maize

Table 4.2 Instantaneous radiation conversion coeffecients for maize (e) calculated from light response curves measured on 3 occassions (23, 43 and 85 DAS) during the S9596 season.

Treatment	Radiation conversion coeffecients (umol CO_2 m^{-2} s-1 umol PAR m^{-2} s^{-1})			Average	Standard error
	23 DAS	43 DAS	85 DAS		
Cg0%	0.059	0.056	0.046	0.054	0.004
Cg25%	0.058	0.064	0.051	0.058	0.004
Cg50%	0.06	0.066	0.065	0.064	0.002
CTd	0.054	0.027	0.002	0.04	0.011

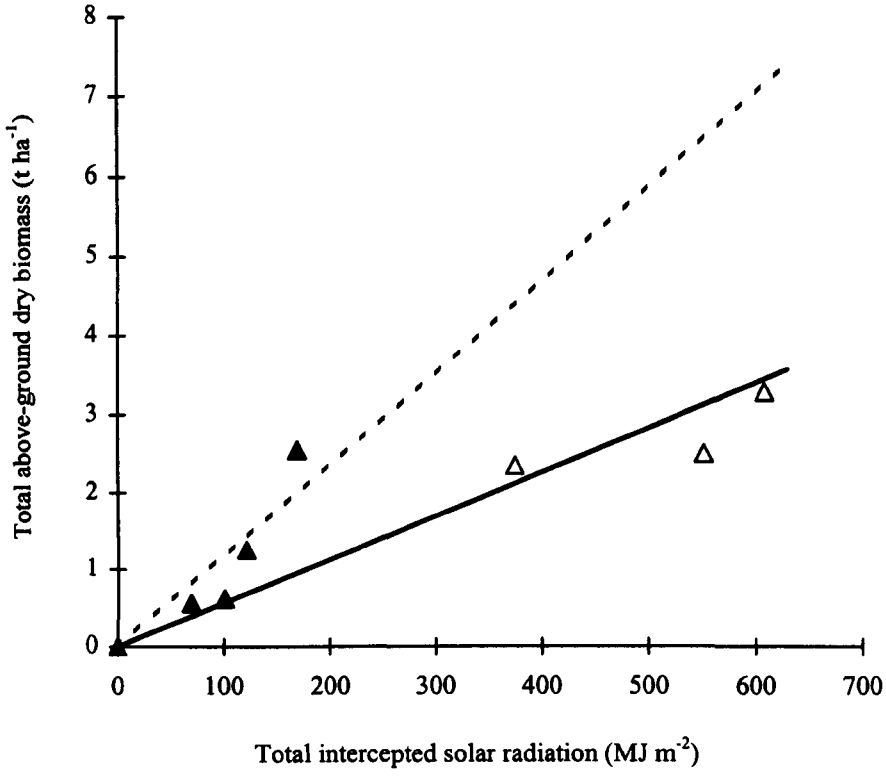


Figure 4.13 Radiation conversion coeffecients (e), represented by the slope of the linear regressions, for Cg 0% maize calculated for the entire S94/95 season (solid line; all symbols) and for the period between emergence and anthesis (dashed line; open symbols only).

than in the sole maize treatments and increased with the intensity of artificial shade (Table 4.2). Empirical estimates of *e* between planting and harvest during S94/95 are shown in Table 4.1. The treatments containing grevillea provided the highest values for *e* of c. 0.7 g MJ^{-1}, which is within the range estimated for forest ecosystems (Black and Ong, 1998). Muchow (1989) reported values for irrigated and water-stressed maize of 1.2 and 0.8 g MJ^{-1} respectively, while (Squire, 1990) suggested values of up to 2.5 g MJ^{-1} for tropical C4 cereals under favourable conditions. The values obtained for sole and agroforestry maize of 0.52 and 0.63 g MJ^{-1} respectively are therefore comparatively low, probably because the planting density, which was chosen with the intention of maximising yield under conditions of limited seasonal rainfall, was sub-optimal for this unusually wet season. Stirling *et al.* (1990) and others have shown that *e* may vary substantially within a single season, with marked differences being associated with the pre- and post-anthesis periods, highlighting the effects that maturation and senescence may have on the calculated values for this parameter. Such variation has been incorporated into growth models including PARCH (Bradley and Crout, 1994) and CERES-Maize (Jones and Kiniry, 1986), with different values for *e* being defined for specific growth stages. Figure 4.13 and the final column of Table 4.1 clearly show that higher *e* values were obtained for the pre-anthesis period than for the entire season, and that this recalculation reversed the ranking of values for maize in the Cg and CTdm treatments.

CHAPTER 5

WATER USE

Water use by the trees and crops was determined using a combination of sap flow and infrared gas analysis (IRGA) methodology (Nottingham), and soil water balance and deuterium labelling techniques (Institute of Hydrology). In the Nottingham studies, constant temperature heat balance gauges (cf. Section 2.5) were used to measure sap flow through the stem and hence transpiration by individual trees or maize plants. IRGA was used to estimate instantaneous water use by maize prior to c. 45 DAS, when the plants were too small to apply sap flow techniques (cf. Section 2.6), or later in the season when the heat balance equipment was being used for trees. The heat balance method was also adapted for use with lateral tree roots (cf. Sections 2.5.4 and 5.4).

5.1 GREVILLEA - DIURNAL TRENDS, DAILY TOTALS AND PLOT LEVEL ESTIMATES

Diurnal timecourses for mean sap flow through the trunks of grevillea trees at the mid-point of each season during experimental years 3-5 (1993/94-1995/96) are shown in Figure 5.1 for the sole (Td) and dispersed agroforestry (CTd) treatments. The diurnal trends for sap flow were similar in both treatments and generally increased rapidly after sunrise (c. 0700 h) to reach a maximum between 1100 and 1300 h before declining again during the afternoon. However, the occurrence of extended dry periods during the cropping season caused the timecourses to become more asymmetric as stress increased (e.g. Fig. 5.1, 1994/95 long growing season). The lowest values were obtained during the dry season, when depletion of soil moisture restricted transpiration and little diurnal variation in sap flow was apparent (Fig. 5.1, 1994/95 dry season).

These diurnal timecourses may be used to calculate cumulative daily and seasonal water use. Figure 5.2 shows daily total sap flow values calculated from measurements made during the standard 12 hour daylight period (0700-1900 h) for Td and CTd trees during four annual cycles (October 1992-September 1996) commencing one year after planting the trees. Sap flow tended to increase from season to season as the trees grew larger, was typically greatest during the short growing season, when the canopy grew rapidly,

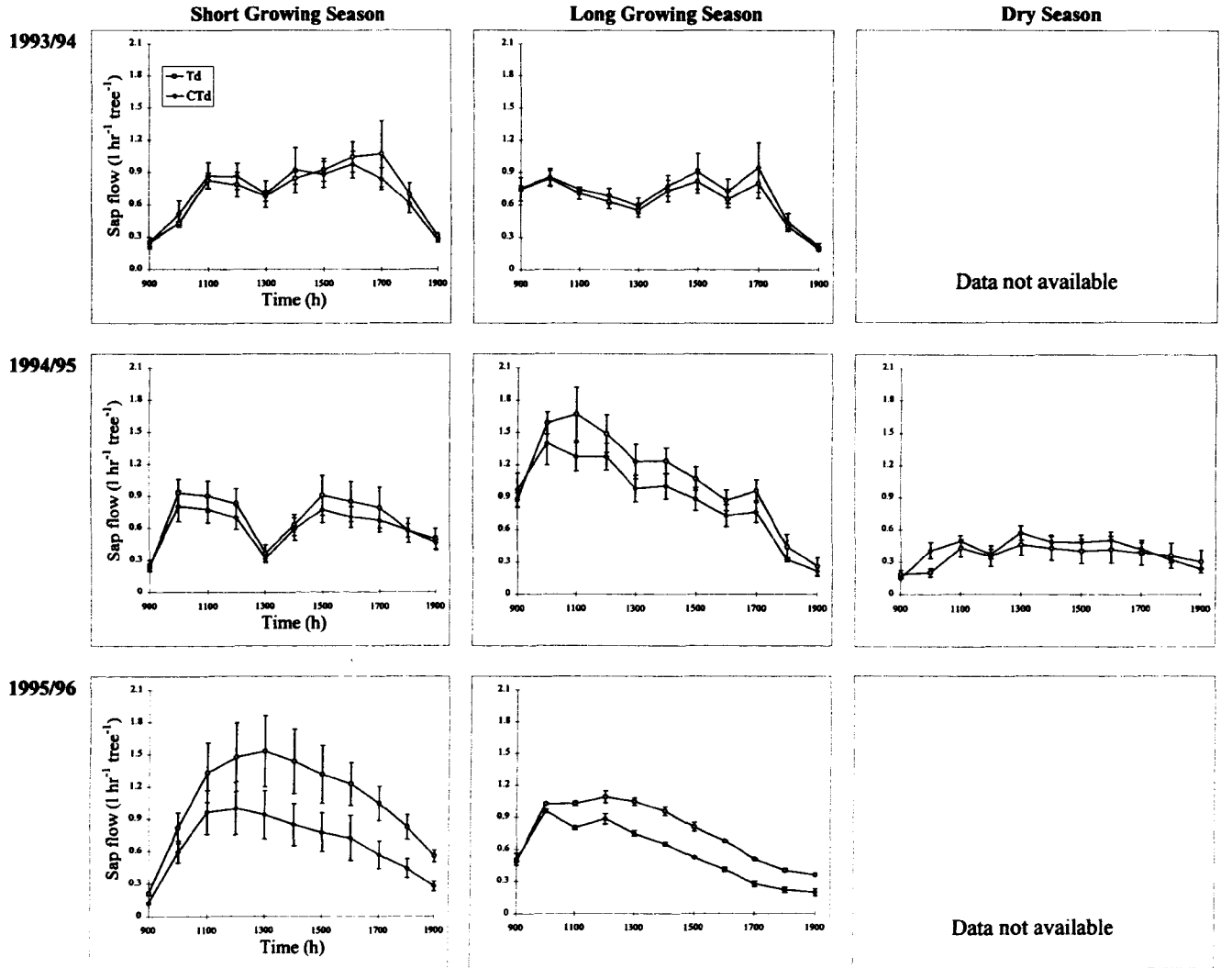
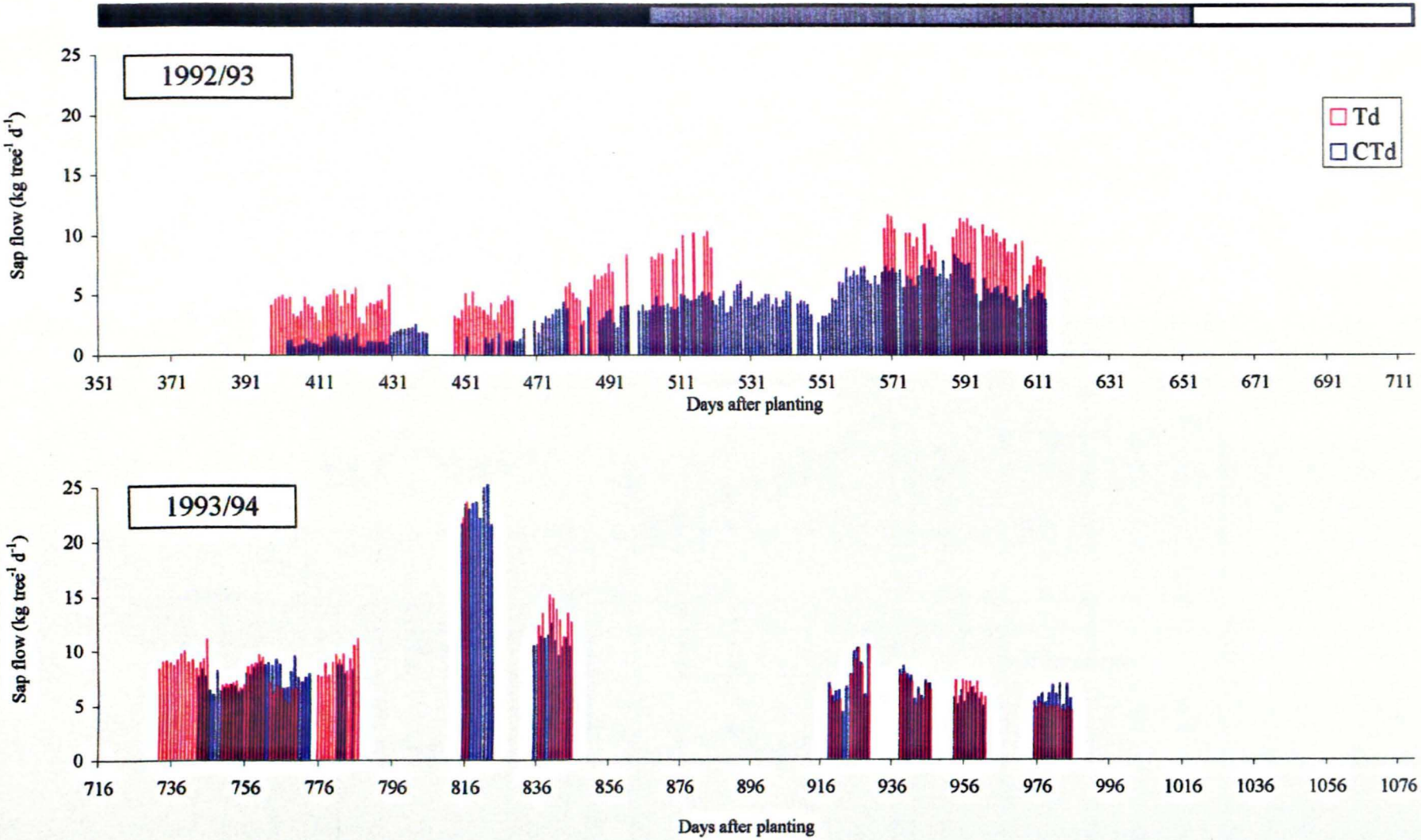


Figure 5.1 Diurnal timecourses of sap flow at the midpoint of the short and long growing seasons and the dry season for trees in the sole (Td) and dispersed agroforestry (CTd) treatments. The data represent the mean of three trees for each treatment on a single day. Double standard errors of the mean are shown.


1992/93
Td
CTd
Sap flow (kg tree^{-1} d^{-1})
Days after planting
1993/94
Sap flow (kg tree^{-1} d^{-1})
Days after planting

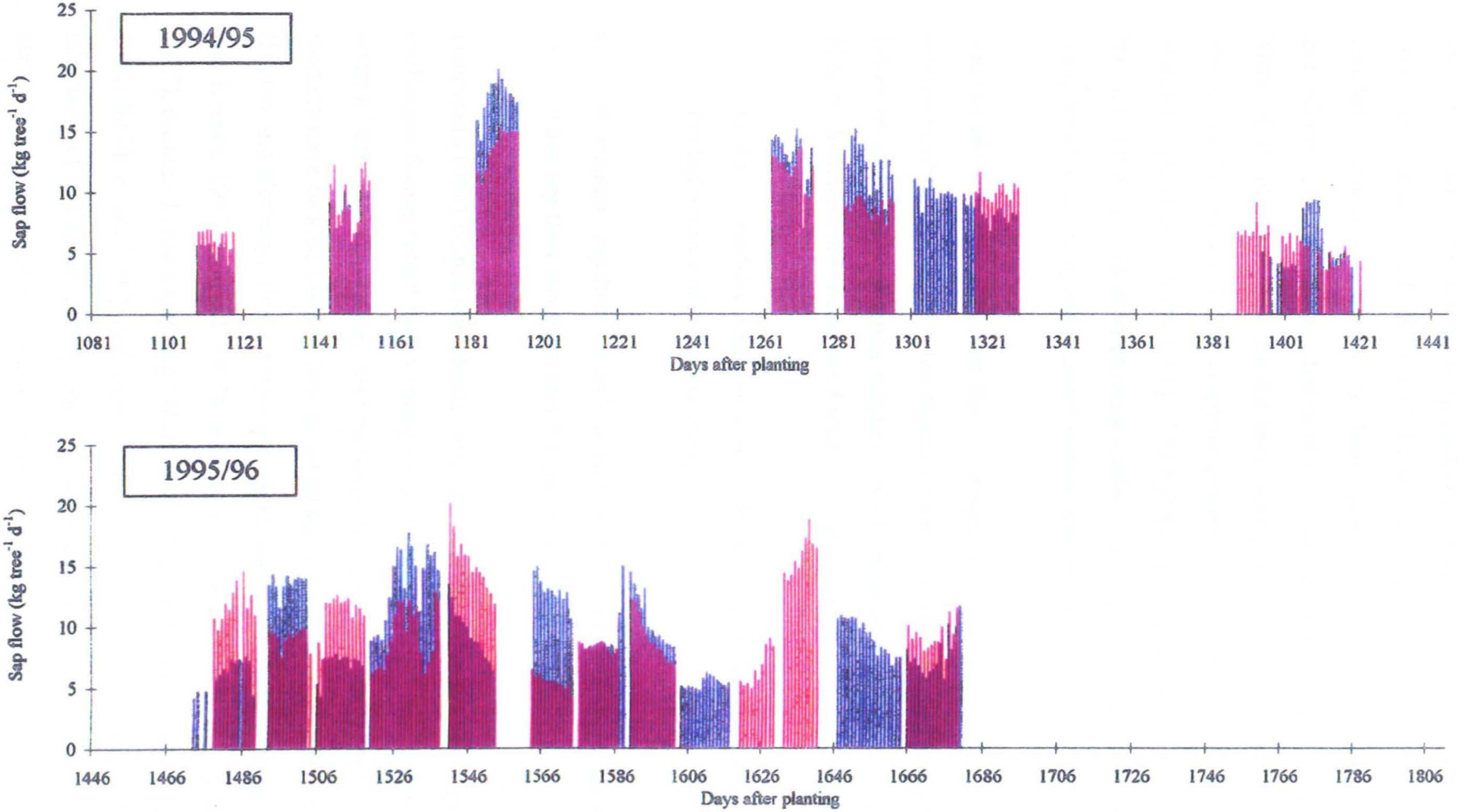


Figure 5.2 Daily total sap flow for grevillea in the sole (Td) and dispersed agroforestry (CTd) treatments during each experimental year. Horizontal bars represent seasons: black, short growing season (Oct-Feb), grey, long growing season (Mar-Jul) and open, dry season (Aug-Sep).

and was not consistently higher in one treatment than in the other. However, the 1992/93 annual cycle did not fully conform to this general pattern since sap flow was consistently greater in Td than in CTd trees. In addition, the values for both treatments reached a maximum during the latter half of the long growing season (L93), immediately prior to pruning, despite the very low rainfall during this season (112 mm). These observations suggest that the trees were able to continue growing and transpiring throughout this unusually dry cropping season by extracting stored soil water at depth within the profile (cf. Section 3.1). The highest sap flow values were recorded towards the end of the 1994/95 short growing season, coincident with the period when leaf area was greatest (Fig. 3.1b) and seasonal rainfall was highest (628 mm).

An intrinsic constraint of all sap flow techniques is that measurements are confined to a limited number of plants and the dataset obtained is often discontinuous because of the laborious and time-consuming nature of the techniques involved. Subsequently, two distinct challenges are encountered when scaling discontinuous sap flow measurements:

i) to obtain stand-level estimates of water use from measurements of sap flow for a limited number of individual trees.

ii) to estimate sap flow for individual trees or stand-level water use during periods when sap flow measurements are not available.

Denmead (1984) coined the phrase 'telling the forest from the trees' to highlight the challenges facing researchers wishing to scale from transpiration by single trees (kg water h^{-1} $tree^{-1}$) to obtain stand-level estimates of water use (mm water d^{-1}). A number of workers have tackled the problem by adopting scaling methods based on tree density (Hatton and Vertessy, 1990), crown size (Ladefoged, 1963), trunk basal area (Cermak and Kucera, 1987; Howard, 1997), total trunk cross-sectional area (Allen and Grime, 1995), estimated crown leaf area (Werk *et al.*, 1988; Allen *et al.*, 1997; Hall and Allen, 1997; Smith *et al.*, 1997), and sapwood area (Thorburn *et al.*, 1993). The success or otherwise of individual scaling methods depended largely on the composition of the stand for which estimates of water use were sought; in the above examples, this ranged

from mono-specific plantations to mixed forests, regular to irregular tree spacings and open to closed canopy structures.

The grevillea trees examined in the present study were regularly spaced, of uniform age and the canopy was open; the principal difference between trees was therefore in size. Smith and Allen (1996) suggested that the most appropriate methods for such stands were those based on relationships between sap flow and an allometric parameter, since these allow area mean transpiration rates to be estimated from surveys of tree size and measurements of sap flow for a limited number of individuals. Methods based on sap flow/leaf area relationships and stand level LAI constitute the most effective approach (Allen and Grime, 1995) provided frequent estimates of leaf area are available. Since leaf area was measured regularly in CIRUS (cf. Section 3.1), water use by individual trees could be scaled to obtain stand level values on the basis of estimated leaf area and stand LAI (cf. Fig. 3.1b) during periods when sap flow measurements were available using:

$$T = \sum_{i=1}^{n} \left(\frac{J_i \times L}{A_i} \right) \frac{1}{n} \qquad \text{Equation 5.1}$$

where T represents stand level transpiration (mm h^{-1}), J_i is the measured trunk sap flow (kg h^{-1}) for the *i*th tree, L is the LAI of the stand and A_i is the estimated total leaf area of the *i*th tree.

The accuracy of stand-level estimates of water use based on sap flow/leaf area relationships depends on two assumptions being successfully satisfied (Hatton and Vertessy, 1989; Olbrich *et al.*, 1993; Allen and Grime, 1995; Hatton and Wu, 1995). These are that:

i) there is a good linear relationship between sap flow and leaf area for all trees in the stand;
ii) all trees within the stand respond similarly to the prevailing environmental conditions.

The first assumption highlights the tight coupling between leaf area and transpiration, which is essential to the pipe model (Shinozaki *et al.*, 1964; Valentine, 1985; Rennolls, 1994; cf. Section 2.4.1.1) and hydrological equilibrium theories (Eagleson, 1982; Nemani and Running, 1989). This assumption was investigated by comparing the correlation coefficients between linear regressions of mean sap flow and median leaf area for each replicate tree during each measurement period (Table 5.1); a method previously adopted by Allen and Grime (1995). Approximately 70 % of the correlations were high (>0.70), with the poorest correlations being obtained in the CTd treatment and during the short growing season, the wettest period of the year. Further analysis revealed that these poor correlations were obtained during dry spells, which were immediately preceded by periods of rapid leaf area expansion in response to heavy rainfall. Under these environmental conditions, short-term hydrological disequilbrium can occur in trees growing on areas of drier or shallower soil. These trees would experience water stress more rapidly than other trees better supplied with water and consequently, the sap flow of the 'early-stressed' trees would be lower on a unit leaf area basis. This results in a decline in the linearity of the relationship between sap flow and leaf area when plotted through measurements collected on all replicate trees, with the extent of the decline being proportional to the severity of water stress experienced by individual trees. The 1995 dry season (D95) appeared to have little effect on the linearity of the sapflow/leaf area relationships. This was probably because sap flow was measured only during the latter part of the dry season (August-September), by which time canopy size in all replicate trees was realigned to the available water supplies by leaf senescence and abscission. As a consequence good linear correlations between sap flow and leaf area were restored, albeit at lower levels of sap flow than during the wet season. Thus, despite occasional short-term lapses in their reliability, good linear relationships between sap flow and leaf area were obtained across varying environmental conditions and tree ages, thereby satisfying the first requirement for scaling sap flow on the basis of the leaf areas of individual trees and stand LAI as discussed above.

Failure to satisfy the second assumption would be highlighted by poor cross-correlations between the sap flow values for replicate trees during specific measurement periods. Poor cross-correlations would indicate that one of the trees within the group of three

Table 5.1 Correlations coefficients for linear regressions of mean sap flow and median leaf area and cross correlations between the sap flow of replicate trees during S94/95, L95 and S95/96. A dash denotes periods when data were not collected.

Season	Measurement period		Correlation coefficients for linear regressions of sap flow and leaf area		Mean coefficients of cross correlations between sap flow of each replicate tree.	
	From	To	CTd	Td	CTd	Td
S94/95	10/29/1994	07-Nov-94	0.999	0.871	0.80	0.69
S94/95	03-Dec-94	13-Dec-94	0.593	0.874	0.70	0.90
S94/95	11-Jan-95	22-Jan-95	0.914	0.967	0.49	0.93
L95	01-Apr-95	12-Apr-95	0.948	0.697	0.64	0.89
L95	21-Apr-95	04-May-95	0.990	0.830	0.90	0.67
L95	10-May-95	21-May-95	0.902	-	0.92	-
L95	23-May-95	06-Jun-95	0.646	0.999	0.86	0.92
S95/96	04-Aug-95	11-Aug-95	0.852	-	-	0.79
S95/96	15-Aug-95	21/8/95	0.870	-	0.16	-
	15-Aug-95	24/8/95	-	0.944	-	0.55
S95/96	22/8/95	27/8/95	0.993	-	0.76	-
	26/8/95	3/9/1995	-	0.786	-	0.93
S95/96	29/8/95	4/9/95	-	-	0.60	-
	6/9/95	6/9/95	-	0.977	-	-
S95/96	28/10/95	13/11/95	0.695	-	0.94	-
	2/11/95	13/11/95	-	0.884	-	0.32
S95/96	17/11/95	28/11/95	0.465	0.995	0.23	0.48
S95/96	30/11/95	12-Dec-95	0.920	0.977	0.91	0.96
S95/96	14/12/95	01-Jan-96	0.615	-	0.94	0.79
S95/96	04-Jan-96	16-Jan-96	0.925	0.843	0.98	0.91
S95/96	26-Jan-96	06-Feb-96	0.435	0.013	0.88	0.89
S95/96	08-Feb-96	19-Feb-96	0.925	-	0.97	0.28

replicates were responding differently to the prevailing above-ground environmental conditions due either to variation in the availability of water or physiological differences between trees. Both factors were potentially important in CIRUS. For example, soil moisture availability varied greatly within CIRUS due to the variable soil depth (Fig. 2.7), differences in infiltration rate resulting from the undulating micro-topography of the soil surface and the irregular distribution of major rainfall events which are frequently separated by prolonged dry periods. In addition, the grevillea trees were sourced from several local nurseries and might therefore contain a range of genetic material, introducing associated physiological variation. However, despite these potential sources of variation, c. 70 % of the observed cross-correlations between replicate trees were high (>0.7; Table 5.1), indicating that the second requirement for scaling sap flow on the basis of tree leaf area and stand LAI was fulfilled during most periods. Consequently, both assumptions required for scaling sap flow to obtain stand-level estimates of water use using sap flow/leaf area relationships were satisfied for much of the time, although the accuracy of the method could be compromised in the short term, particularly at the onset of dry spells.

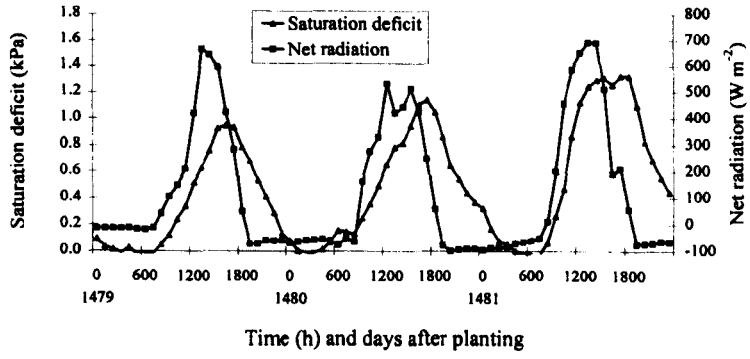
The second challenge in scaling water use is the estimation of stand transpiration during periods when heat balance measurements were not made. Allen and Grime (1995) estimated sap flow for periods when data were missing (equivalent to c. 25 % of the overall sampling period) by linear interpolation using the total basal stem cross-sectional area of the trunks. However, the variable nature of the prevailing environmental conditions at Machakos, and the length of time between some sapflow measurements, would seriously undermine the validity of using this approach for CIRUS. Transpiration is often closely coupled to net radiation in the absence of water stress (Jones, 1992) because radiation provides the primary source of energy driving evaporation. As a result, much of the intercepted solar energy is dissipated as latent heat of vaporisation provided there is free movement of water between the energy-absorbing surface and the atmosphere. However, when transpiration is limited by a low saturation deficit, stomatal closure or limited soil water availability, the proportion of the intercepted radiant energy dissipated as thermal radiation increases, primarily by convection, and the coupling of sap flow to net radiation deteriorates. Consequently the difference between potential and actual transpiration under dryland conditions is

strongly influenced by the balance between soil water availability and transpirational demand.

Diurnal timecourses for net radiation, saturation deficit and sap flow (expressed as mean sap flow per tree, or per unit leaf area, or as the total for the stand) in Td and CTd grevillea during three consecutive days in 1994 following either copious (113 mm of rain during the preceding 14 days) or limited rainfall (9 mm during the previous three months) are shown in Figures 5.3 and 5.4. The diurnal timecourses for saturation deficit and net radiation were similar during both periods, although net radiation tended to be greater and saturation deficit lower following the heavy rainfall period. Sap flow tracked the timecourse of net radiation to reach a maximum around noon during both measurement periods, although the absolute values were much lower during the period following low rainfall. Other workers (e.g. Schulze *et al.*, 1985; Green and Clothier, 1988; Hatton and Vertessy, 1990) found that flow in well-watered trees lagged behind net radiation by up to 1.5 hours, which Hatton and Vertessy (1990) attributed to the time lapse between sap flow at the measurement height (breast height or 1.5 m) and transpiration by the canopy. However, as the heat balance gauges were installed immediately below the canopy during the measurements shown in Figures 5.3 and 5.4, the potential for lag between sap flow at the measurement point and transpiration from the canopy was minimised. The timecourse for sap flow tended to precede that for saturation deficit, which peaked during the latter part of the daylight period, between 1700-1800 h. The larger standard errors for sap flow during the dry period reflect the increased variation between replicate trees at this time, probably caused by local variation in soil depth and hence the availability of residual water to support transpiration.

Normalising sap flow for leaf area and scaling to provide estimates of stand-level water use reduced the standard errors associated with these measurements in both treatments (Figs. 5.3c and d; Figs. 5.4c and d), except for CTd trees during the wet three-day period, and resulted in closer agreement between the values for both treatments. This observation substantiates the earlier conclusion that the total leaf area of individual trees and stand LAI are suitable parameters for scaling sap flow to provide stand-level estimates of water use. The larger standard errors obtained when sap flow in CTd trees

a)



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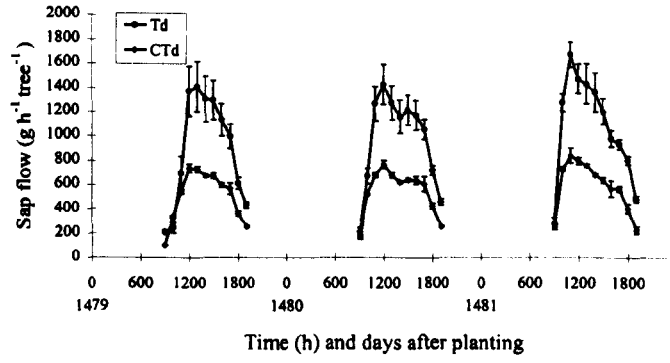

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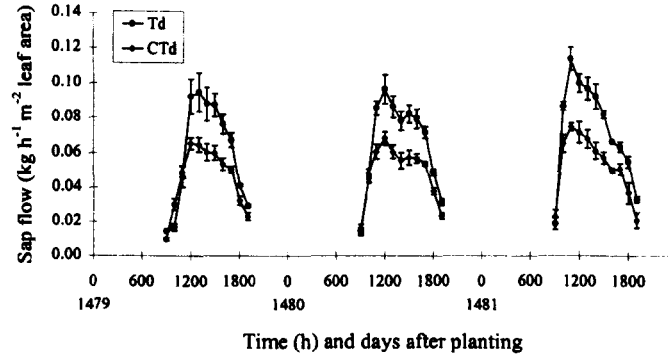

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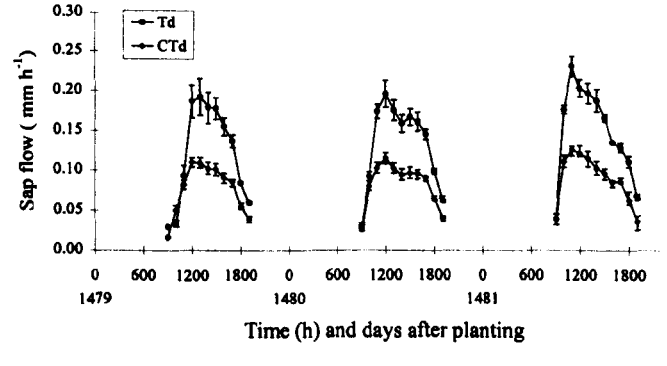
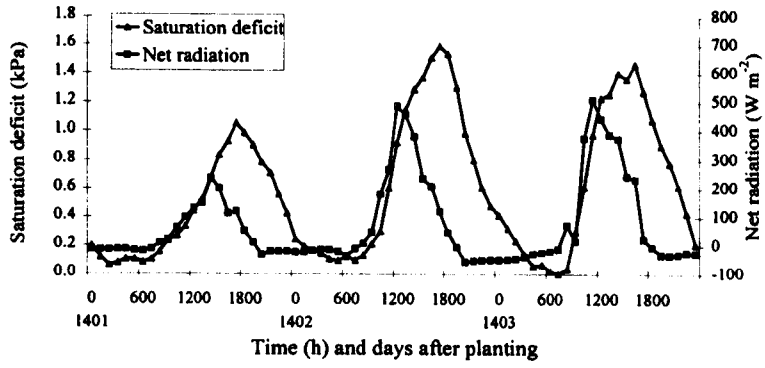


Figure 5.3 Diurnal timecourses on three consecutive days in November 1995 for a) saturation deficit and net radiation, and sap flow in the sole (Td) or dispersed agroforestry (CTd) treatments measured on the basis of b) individual trees, c) m^2 leaf area and d) the stand. Double standard errors of the mean area shown. The period of measurement was relatively wet, with 113 mm of rain received during the previous 14 days.

a)



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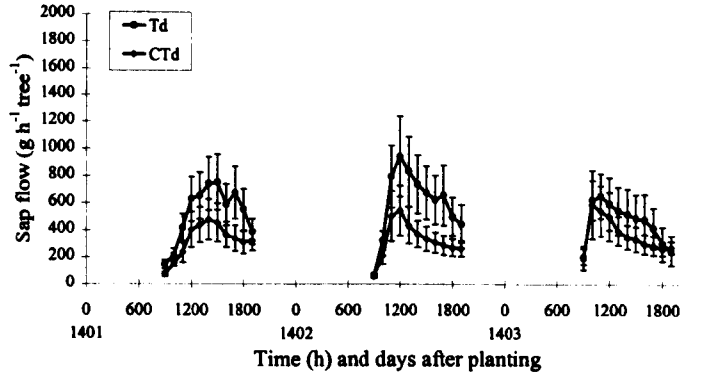

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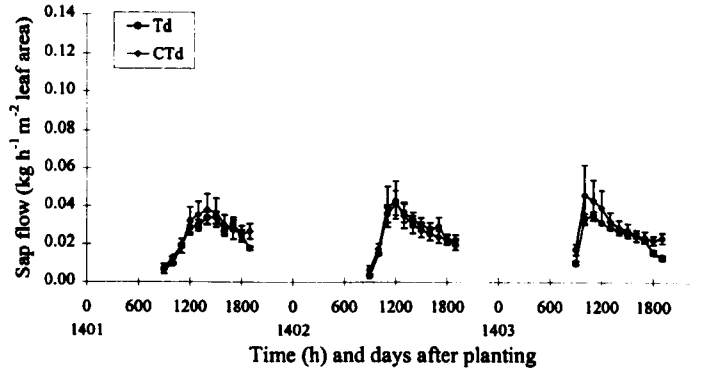

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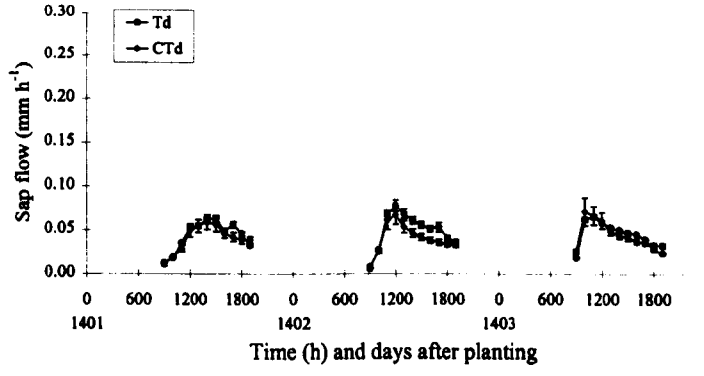

Figure 5.4 Diurnal timecourses on three consecutive days in August 1995 for a) saturation deficit and net radiation, and sap flow in the sole (Td) or dispersed agroforestry (CTd) treatments measured on the basis of b) individual trees, c) m^2 leaf area and d) the stand. Double standard errors of the mean are shown. Measurements were made following an extremely dry period; 9 mm of rain had been received during the preceeding 3 months and no rain during the previous 14 days.

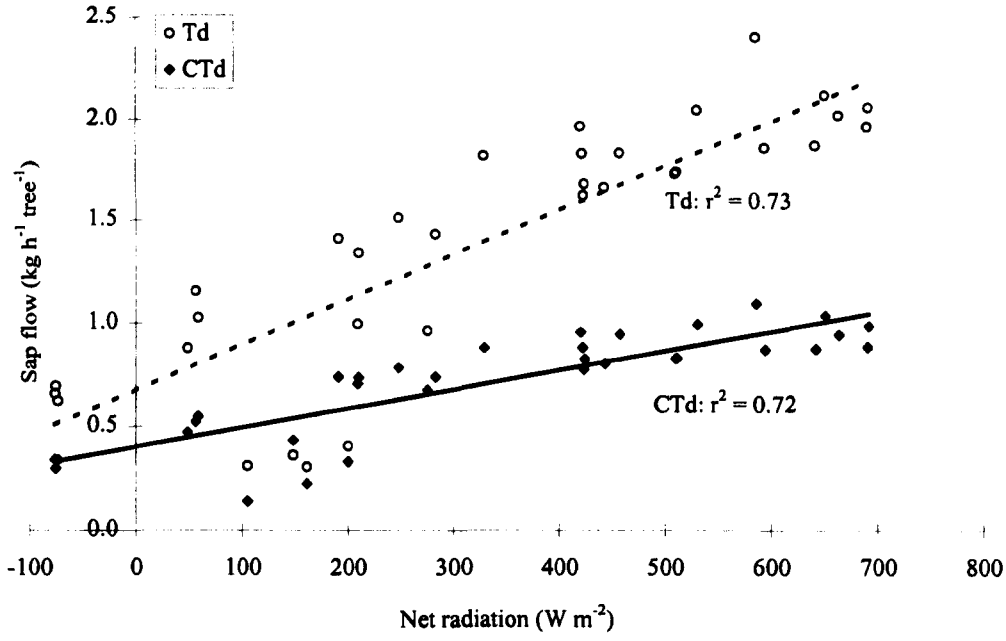

Figure 5.5 Relationship between net radiation measured above the tree canopy and sap flow in the sole (Td) and dispersed agroforestry (CTd) treatments during the wet three day period referred to in Figure 5.3.

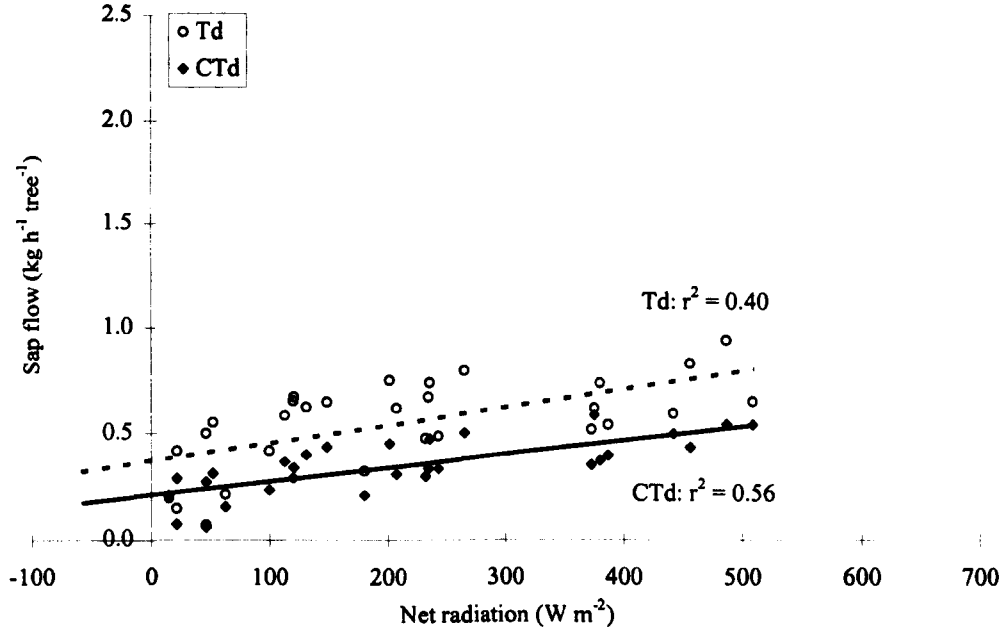

Figure 5.6 Relationship between net radiation measured above the tree canopy and sap flow in the sole (Td) and dispersed agroforestry (CTd) treatments during the dry three day period referred to in Figure 5.4.

was expressed on a leaf area basis during the wet three-day period suggests that transpiration may have been source-limited. This conclusion was supported by the values for sap flow per tree, which differed little despite the c. 65 % difference in leaf area between replicate trees.

The close coupling between stand level water-use and net radiation is shown in Figures 5.5 and 5.6 for both of the three-day periods referred to above. The relationship between transpiration and net radiation was much closer in both treatments during the wet three day period (Fig. 5.5) and was steeper in the Td treatment, reflecting the greater limitation on water availability in the CTd treatment during cropping seasons. During the wet three day period, the correlation coefficients for both treatments were improved considerably (r^2 = 0.85 and 0.83 for Td and CTd respectively) if the 9 a.m. values were omitted from the analysis. This may provide evidence for the existence of a lag between the onset of transpiration and the consequent increase in sap flow at the measurement height due to the build up of stored water in the canopy over night, or to the occurrence of lower transpiration rates early in the day when air temperature and saturation deficit are relatively low. Green and Clothier (1988), Hatton and Vertessey (1990) and Howard (1997) also found good correlations between transpiration and net radiation which therefore supports the view that net radiation is a suitable parameter for scaling water use when water supplies are non-limiting. Howard (1997) used a series of relationships between sap flow in grevillea in CIRUS and solar radiation to gap-fill between successive heat balance measurements for periods of up to four months during the first 2.5 years of the experiment. However, when the three-day periods referred to above were extended to include more days, ten for example, the reliability of the correlations between sap flow and net radiation decreased dramatically. This observation highlights the complexity of the relationship between transpiration and net radiation under highly variable field conditions and seriously undermines the reliability of using net radiation as the sole predictive parameter for estimating sap flow. For example, other factors which directly affect transpiration such as saturation deficit and soil surface moisture content varied by up to 0.5 kPa and 7.5 % respectively in the Td treatment over periods of ten consecutive days in CIRUS (Wallace *et al.*, 1995). Howard's method for scaling water use was probably justified during the early stages of the experiment since the trees were able to exploit water reserves deep within the soil profile, particularly during the

1993 dry season (D93) when the surface horizons were much drier. This argument was supported by the observation that the growth rate of above-ground tree biomass was greater in both the Td and CTd treatments during the dry season than during the preceding short or long growing seasons (Fig. 3.4e). As residual water at depth became depleted during the later stages of the trial, the difference between potential and actual transpiration during dry periods would have been determined increasingly by the balance between soil water availability and evaporative demand, and the physiological responses of the trees. Since these factors vary continually, methods for scaling water use by trees between periods when sap flow was measured must be based on relationships that take account of the changing availability of energy and water, as well as adaptive plant responses.

Scaling methods should ideally maintain the complete independence of measurements of transpiration by the trees from other components of the water balance (Hatton and Vertessy, 1990). This has been achieved for trees growing in humid environments (e.g. Tournebize *et al.*, 1996; Allen *et al.*, 1997) where limitations in water supply are rare, which therefore allows scaling methods to concentrate exclusively on factors of atmospheric energy supply and demand. However, the impact of soil water availability on transpiration by trees growing in semi-arid environments cannot be ignored. Consequently, researchers who have examined the impact of either short or long-term limitations in water supply on tree water use (e.g. Hatton and Wu, 1995; Hall and Allen, 1997) have therefore included parameters describing the soil water deficit in their analyses. Attempts were made in the present study to estimate soil water deficits using time-decay functions since the previous rainfall (data not presented), but these proved unsuccessful. As the work reported here formed part of a larger collaborative study in which continuous measurements of soil moisture were made by Institute of Hydrology staff, the necessary data will eventually become available to support these analyses. Further work on the scaling of tree water use between successive sap flow measurement periods will therefore be postponed until analysis of these data has been completed.

Figure 5.7 illustrates the water use of grevillea during the final two experimental years (1994/95 and 1995/96) scaled to provide plot-level estimates using equation 5.1. The general trend for transpiration was similar in both years, reaching a peak towards the end

of the short growing season at the time of maximum leaf area (cf. Fig. 3.1b), and thereafter declining as a consequence of tree pruning and diminishing soil moisture availability. Both treatments followed similar timecourses, although the values for the Td treatment tended to increase more rapidly following the onset of the rains at the beginning of each experimental year, illustrated by the large difference between Td and CTd transpiration during the first measurement period. Mean transpiration rates were significantly greater in both treatments during the S94/95 short growing season than during the S95/96 season ($p<=0.01$). Maximum transpiration rates during 1994/95 reached a mean for both treatments of 4.1 mm d^{-1} compared to 2.6 mm d^{-1} during 1995/96. The higher maximum values recorded during 1994/95 may reflect the combination of more favourable soil moisture conditions resulting from the greater rainfall received during S94/95 (628 *vs.* 317 in S95/96) and the greater leaf area of the trees (cf. Fig. 3.1b). During the dry season (D95), the mean transpiration rate was 0.6 mm d^{-1} in both treatments, less than 40 % of the mean values for the short growing seasons referred to above.

In a review of the available information concerning the water requirements of forest trees, Rutter (1968) concluded that water use rates of 1-2 mm d^{-1} were typical for trees experiencing conditions similar to those in CIRUS (moderate to severe water stress and an annual precipitation of 500-800 mm). More recent studies using sap flow gauges include Miller and Poole (1979), who recorded maximum values of 0.7-2.0 mm d^{-1} for various desert shrub species and Allen and Grime (1995) who reported values of 1.5-2 mm d^{-1} for savannah shrubs. Allen *et al.* (1997) observed daily mean transpiration rates of 5.0 and 2.4 mm d^{-1} for two poplar varieties grown in the UK during wet periods, whereas the values declined to 1.9 and 1.6 mm d^{-1} during dry periods. The mean transpiration rates recorded in the present study therefore compare favourably with those reported for a range of tree species growing in both water-limited and seasonally water sufficient environments.

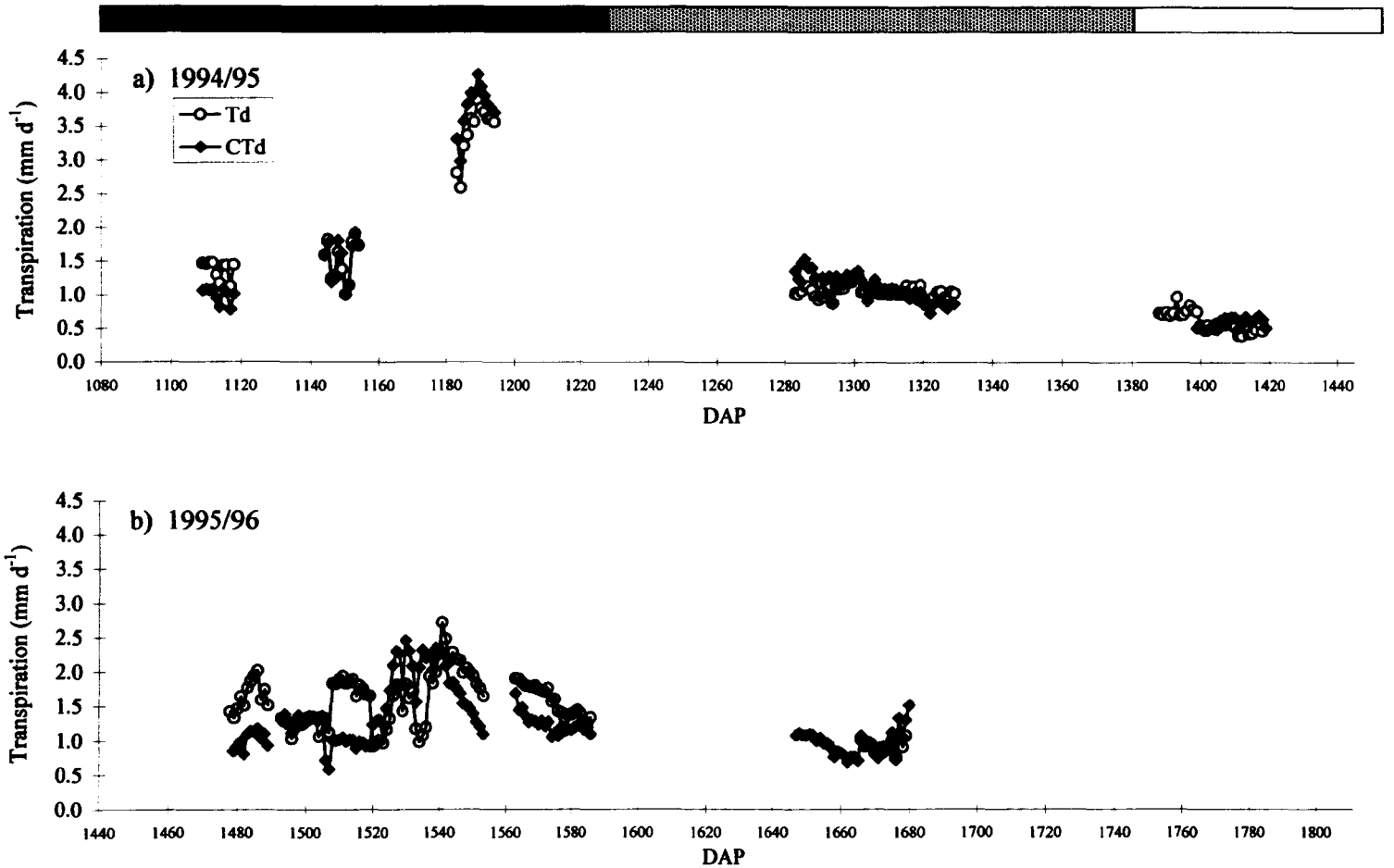

Figure 5.7 Stand level transpiration for grevillea in the sole (Td) and dispersed agroforestry treatment (CTd) during a) 1994/95 and b) 1995/96 experimental years. DAP refers to the number of days after tree planting.

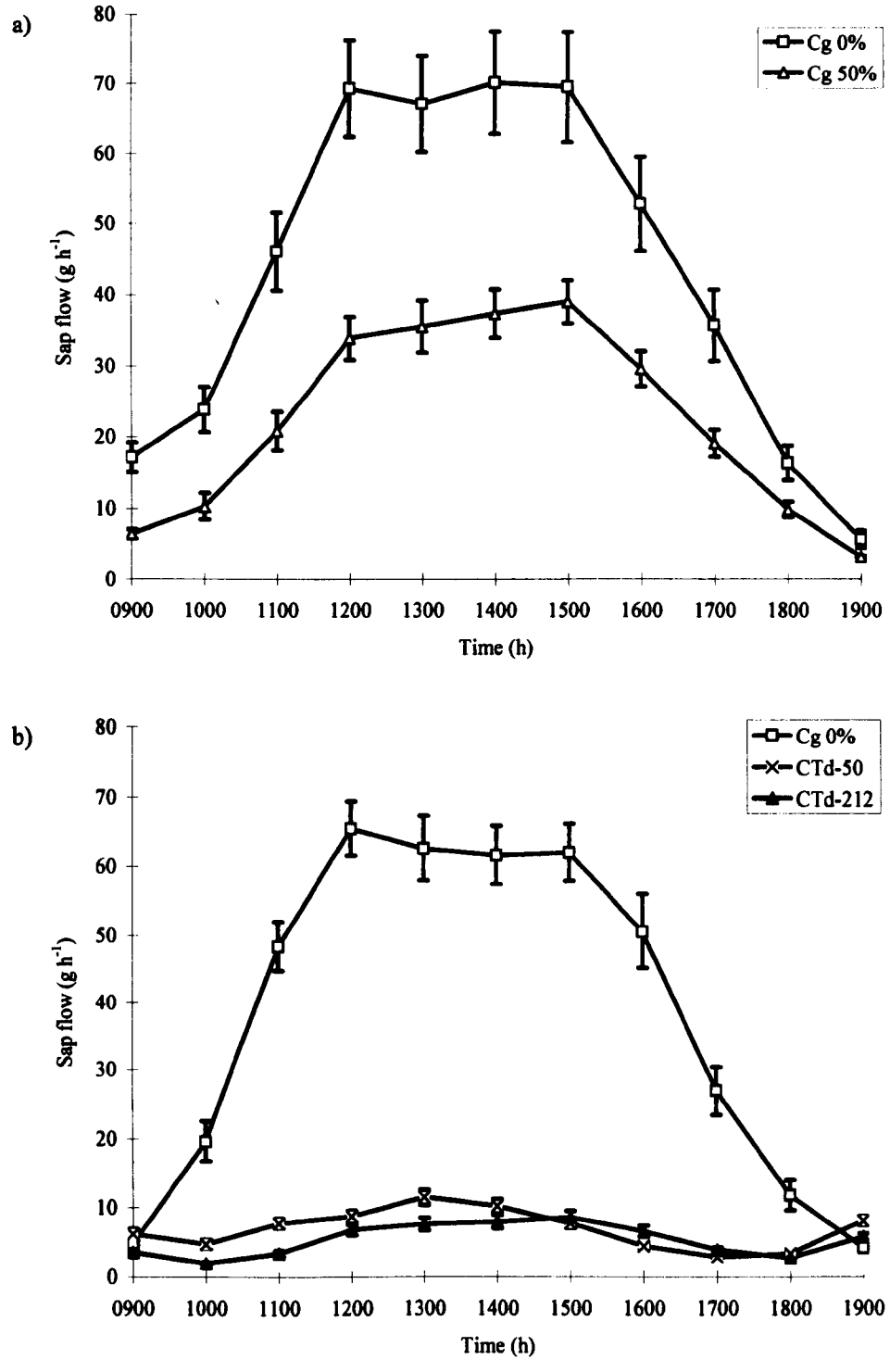

Figure 5.8 Diurnal timecourses of sap flow in maize during the 1995 long growing season. a) Impact of 50 % artificial shade on transpiration by maize (Cg 50%) relative to the unshaded control (Cg 0%) and b) effect of grevillea on transpiration by maize at distances of 50 (CTd-50) and 212 (CTd-212) cm from the nearest tree. Double standard errors of the mean are shown except where these are smaller than the symbols.

5.2 MAIZE - DIURNAL TRENDS, DAILY TOTALS AND SCALING TO OBTAIN PLOT LEVEL ESTIMATES

Figure 5.8 shows typical diurnal timecourses for sap flow in maize grown as an unshaded sole crop (Cg 0%) or under 50 % artificial shade (Cg 50%), or in the CTd treatment at distances of 50 and 212 cm from the nearest tree at c. 50 DAS during the 1995 long growing season (L95). Sap flow exhibited pronounced diurnal variation in both sole maize treatments, with maximum hourly rates for individual Cg 0% maize plants being <6.5 % of the equivalent value for CTd grevillea (Fig. 5.1). Water use by maize grown under 50 % shade netting was approximately half that of unshaded sole maize, although the diurnal trends were comparable. Water use was almost completely suppressed in CTd maize up to 212 cm from the nearest tree, and maximum flow rates were less than 15 % of those for sole maize. The extremely low water use values are reflected by the severe reduction in CTd maize yields in this season of near-average rainfall (Fig. 3.6c).

Cumulative daily water use by maize may be calculated from the diurnal trends for sap flow in a similar manner to grevillea (cf. Section 5.1). Figure 5.9 shows sap flow values for maize between 40-90 DAS during L95, the longest continuous period of sap flow measurements for maize. Daily water use by unshaded sole maize (Cg 0%) varied greatly, reflecting day-to-day variation in climatic conditions and soil water availability, and was significantly greater ($p<=0.01$) than in maize grown under 50 % artificial shade (Cg 50%). Water use by the CTd maize was significantly greater 50 cm from the trees than at 212 cm (Fig. 5.7b; $p<=0.01$). This effect may be explained by the frequently greater soil water content close to trees after major rain events as a consequence of the interception of precipitation by the tree canopy and the subsequent focusing of rainwater around the base of the trunk by stem flow (N. Jackson, pers. comm.).

Sakuratani (1987) used the product of mean sap flow, measured using the heat balance method, and plant density to estimate transpiration per unit land area. However, in a comparison of scaling methods, Ham *et al.* (1990) found that the use of plant density as a scaling factor for cotton was unsatisfactory since it resulted in an overestimation of transpiration which was attributed to high plant-to-plant variability; similar variability

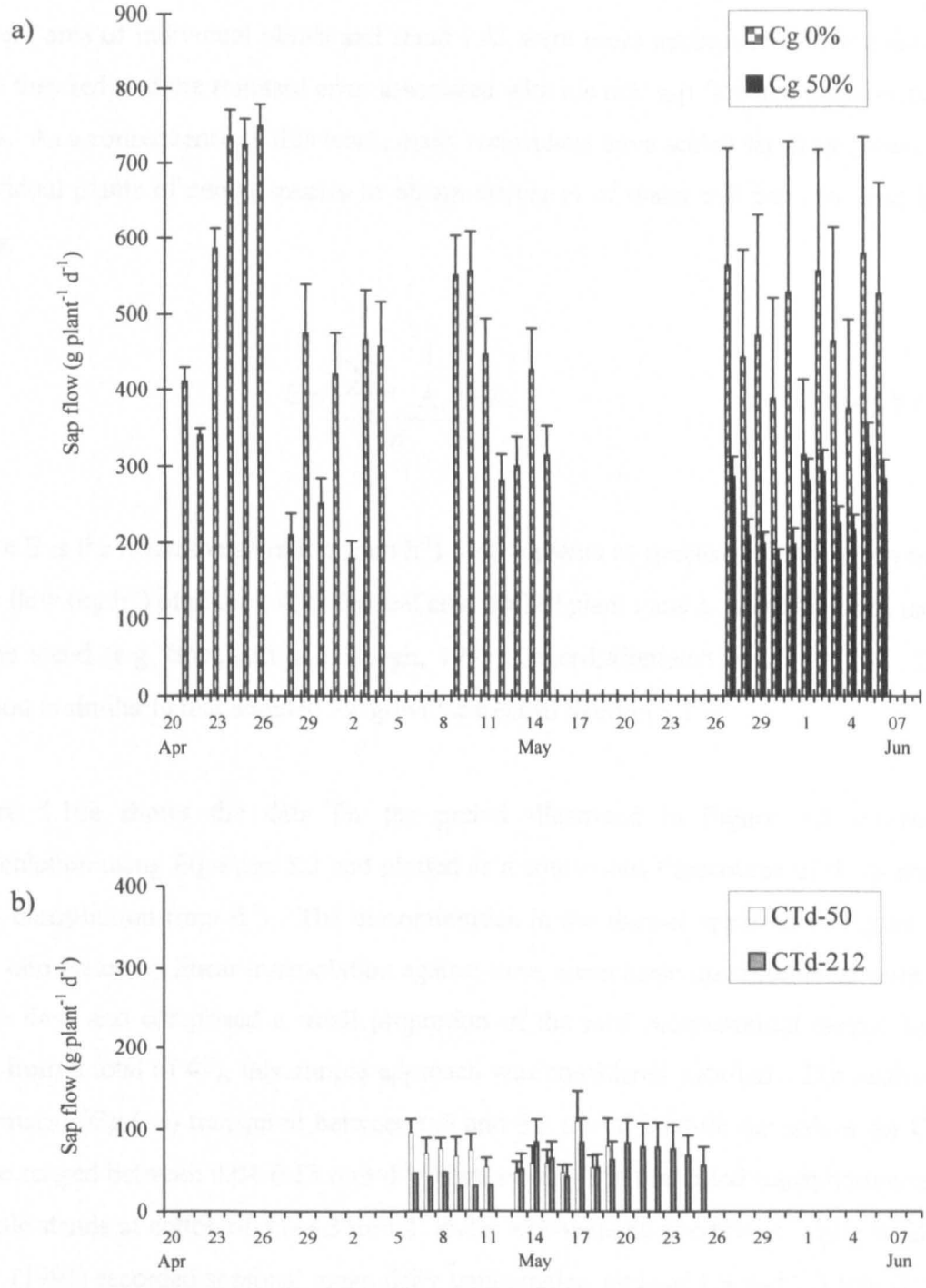

Figure 5.9 Total daily sap flow in maize during the 1995 long growing season. Impact on transpiration relative to the unshaded control (Cg 0%) of a) sole maize grown under 50% artificial shade (Cg 50%) and b) maize grown in the CTd agroforestry treatment at distances of 50 (CTd-50) and 212 (CTd-212) cm from the nearest tree. Double standard errors of the mean are shown.

was also observed between CTd maize plants. These workers therefore proposed that the leaf area of individual plants and stand LAI were more appropriate scaling factors since they reduced the standard error associated with the raw sap flow measurements by 50 %. As a consequence of this work, many researchers have scaled sap flow values for individual plants of cereal species to obtain estimates of water use per unit land area using:

$$E = \left(\frac{\sum_{i=1}^{n} \frac{J_i}{A_i}}{n} \right) \times L \qquad \text{Equation 5.2}$$

where E is the mean transpiration (mm h^{-1}) from n plants of species i, J_i is the measured stem flow (kg h^{-1}) of plant i, A_i is the leaf area (m^2) of plant i and L is the leaf area index of the stand (e.g. Soegaard and Boegh, 1995; Ozier-Lafontaine *et al.*, 1997). This method is similar to that adopted for grevillea trees in Section 5.1.

Figure 5.10a shows the data for the period illustrated in Figure 5.9 following recalculation using Equation 5.2 and plotted as a continuous timecourse of daily stand-level transpiration (mm d^{-1}). The discontinuities in the dataset apparent in Figure 5.9 were eliminated by linear interpolation against time; since these discontinuities were for single days and comprised a small proportion of the total measurement period (three days from a total of 47), this simple approach was considered justified. The unshaded sole maize (Cg 0%) transpired between 0.5 and 3.5 mm d^{-1}, while the values for CTd maize ranged between 0.04-0.18 mm d^{-1}. Ham *et al.* (1990) reported transpiration rates for sole stands of cotton of 3.0-4.3 mm d^{-1} under well watered conditions, while Wallace *et al.* (1991) recorded seasonal mean daily transpiration rates of 1.9 and 2.3 mm d^{-1} for intercropped and irrigated maize during two consecutive growing seasons in the tropical environment of Mauritius; the average seasonal range was 0.5-4 mm d^{-1}. Both studies used sap flow measurements to estimate daily stand-level transpiration and the range of values obtained was similar to that for sole maize in CIRUS. The timecourse for daily transpiration by sole maize tracked those for saturation deficit (Fig. 5.10c) and solar radiation (Fig. 5.10d) reasonably closely between 40-75 DAS, but thereafter there was no clear correlation, probably because the lower frequency and intensity of rainfall

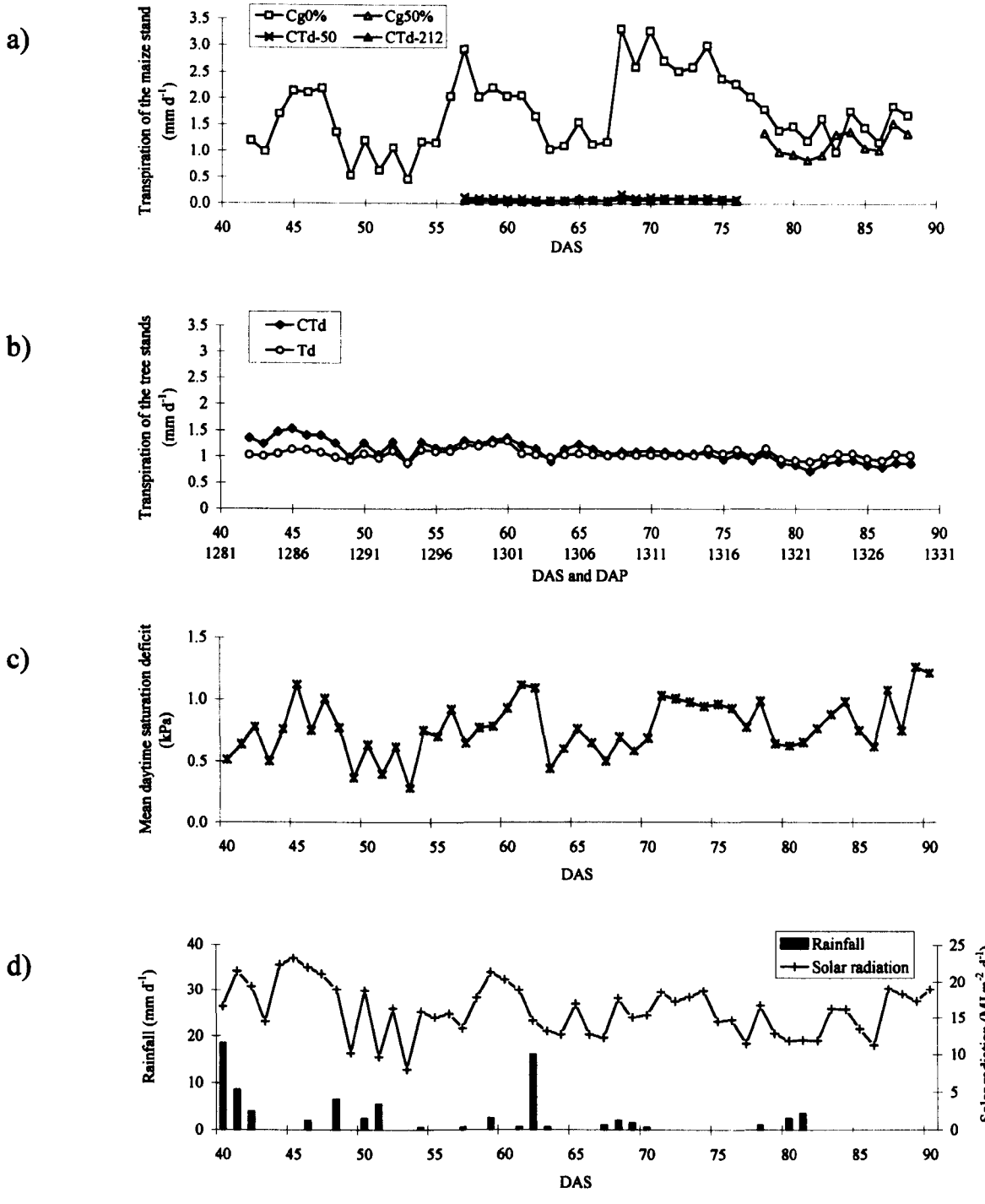

Figure 5.10 Daily mean values for a) transpiration of maize stands grown as a sole crop (Cg 0%), under 50 % artificial shade (Cg 50%) or in the agroforestry treatment at 50 cm (CTd-50) or 212 cm (CTd-212) from the nearest tree; b) transpiration of grevillea in the sole (Td) and dispersed agroforestry (CTd) treatments; c) mean daytime saturation deficit; and d) daily total rainfall and solar radiation. The measurements were recorded during the 1995 long growing season from 40 to 90 days after sowing (DAS) the maize crop or 1281 to 1331 days after tree planting (DAP).

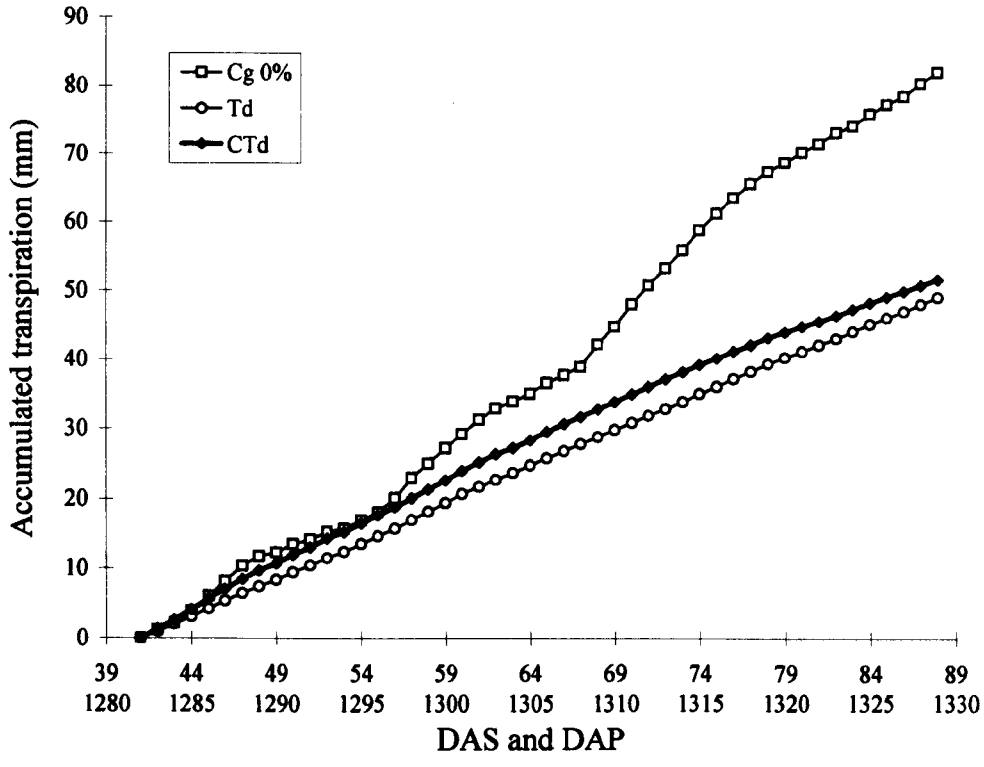

Figure 5.11 Accumulated stand level transpiration for sole maize (Cg 0%) and grevillea in the sole (Td) and dispersed agroforestry (CTd) treatments during the 1995 long growing season between 41 and 88 days after sowing (DAS) the maize crop, or 1281-1331 days after tree planting (DAP).

Table 5.2 Instantaneous water use ratios (mg CO_2 g^{-1} H_2O) for each treatment during the 1995/96 short growing season.

Treatment	DAS		
	25	43	85
Cg 0%	10.4	7.6	11.5
Cg 25%	12.5	15.8	9.3
Cg 50%	14.4	34.5	11.6
CTd	11.9	9.3	6.9
Mean	12.3	16.8	9.8
SE	0.8	6.2	1.1

during the second half of the measurement period reduced soil water availability. This hypothesis is supported by the relatively low harvest indices recorded during L95 (Fig. 3.6), suggesting that the high transpirational demand created by the luxuriant vegetative growth during the early part of the growing season could not be sustained during grain set and grain filling, thereby limiting grain yield.

Figure 5.10b shows a continuous timecourse for daily transpiration by grevillea in the Td and CTd treatments for the same period as shown for maize in Figure 5.10 a; these data are repeated from Figure 5.7 to facilitate comparison. Both treatments followed a similar timecourse, with total daily values ranging from 0.8-1.6 mm d^{-1}; the values for CTd trees were slightly higher than those for Td trees during the early stages of the measurement period, but slightly lower towards the end. A general decline in transpiration was apparent in both treatments during the measurement period, probably in response to the general reduction in the quantity and frequency of rainfall.

Figure 5.11 shows cumulative transpiration over a c. 50 day period during L95 for maize in the Cg 0% treatment and grevillea in the Td and CTd treatments. Total accumulated transpiration during this period was significantly greater for unshaded sole maize (82 mm; $p<=0.01$) than for either of the agroforestry treatments (mean of c. 50 mm for the Td and CTd treatments. The value for Cg 0% maize relates to a period when the plants were transpiring at close to their maximal rate as a result of their large green leaf area, the substantial quantity of residual soil water left over from the previous rainy season, and high rainfall during the early part of the current season. During the 40 day period between planting and commencement of the transpiration measurements, the maize plants were small and hence would have contributed relatively little to the seasonal total transpiration. In addition, during the c. 20 day period between the end of the measurement period and final harvest, the plants were senescent and would again have contributed little to the seasonal total water use. Consequently, the total accumulated transpiration for maize of 82 mm shown in Figure 5.11 represents a substantial, but unquantified, proportion of the seasonal total.

As the trees had been pruned 60 days before the transpiration measurements began, their maximal transpiration rates were lower that would be expected at other times of year,

particularly during the short growing season (cf. Figs. 5.2 and 5.7). In addition, the trees would not have been affected by the limitations on transpiration before and after the measurement period referred to above for maize. Thus, although accumulated transpiration by the trees was c .60 % of that for sole maize during the period when sap flow was measured in maize, accumulated transpiration by the trees would be expected to be greater than or at least the same as that of sole maize on an annual or seasonal basis, particularly during the short growing season.

5.3 WATER USE RATIO IN MAIZE

Figure 5.12 shows the relationship between net photosynthetic (Pn) and transpiration rates (Et) for maize in each treatment during the S95/96 season recalculated from the dataset used to construct the photosynthetic light response curves shown in Figure 4.12. Pn generally increased to a plateau, where Pn remained constant as Et continued to increase; this pattern resulted from the light saturation of photosynthesis at high PAR fluxes. Consequently, above the light saturation point, increasing radiation reduced the instantaneous water use ratio (WUR; Pn/Et), as was also reported by Kanemasu (1983) for sorghum growing under water-limited conditions in Kansas. However, the sole maize treatments (Cg 0%, Cg 25% and Cg 50%) did not comply with this pattern early in the season (25 DAS) since Pn and Et both declined at PAR fluxes above light saturation. This was probably because the regulation of water loss by stomatal control was more effective at a time when the plants had a limited number of small and young leaves. As leaves age, they abrade against each other and begin to senesce and thereby allow direct water loss from the mesophyll and through the cuticular layers of the leaf (MacKerron, 1976). Pn and Et were both reduced in CTd maize relative to the sole maize treatments, particularly at 43 and 85 DAS.

The mean ratio of Pn to Et during the initial linear phase of the curves shown in Figure 5.12 provides a measure of the instantaneous water use ratio (WUR), which may be taken as a measure of the 'efficiency' with which water is being used during photosynthesis. The overall mean value for all treatments and sampling dates was 13.0 mg CO_2 g^{-1} H_2O (S.E. 2.1, n=16). At 25 and 43 DAS, WUR increased with increasing shade intensity in the shade net treatments (Table 5.2), indicating that the reduction in

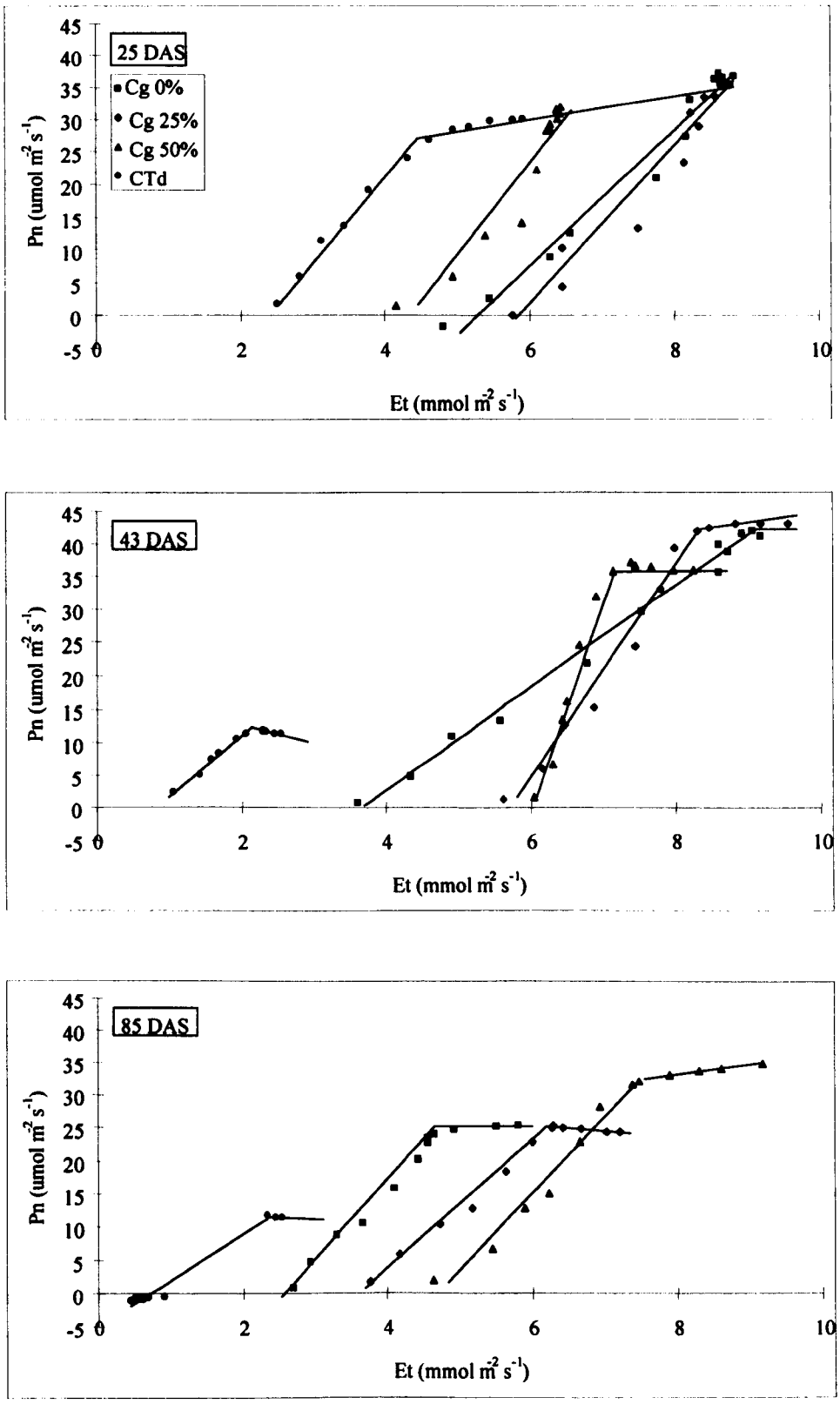

Figure 5.12 Relationship between net photosynthetic rate and transpiration rate for maize grown as a sole crop (Cg 0%), under 25 or 50 % artificial shade (Cg 25% and Cg 50%) or in the dispersed agroforestry (CTd) treatment on three days (25 43 and 85 DAS) during the 1995/96 short growing season.

photosynthesis was smaller than that in transpiration. The values for the CTd maize on both dates were only slightly higher compared to those for unshaded Cg 0% maize. WUR declined sharply between 43 and 85 DAS in all except Cg 0% maize as the plants approached senescence and their photosynthetic competence declined.

5.4 COMPLEMENTARITY OF WATER USE

Previous studies have suggested that grevillea has a high potential for complementarity with crops because its roots are oriented in a predominantly vertical plane and there are few lateral roots within the cropping zone (Plate 5.1a), although these may extend for some distance through the surface horizons. Previous studies to test this hypothesis (Howard, 1997; Howard *et al.*, 1997) involved excavating soil from around individual trees to a depth of 60 cm, the maximum rooting depth of cowpea in CIRUS. The results suggested that grevillea may extract up to 80 % of its water requirements from below the crop rooting zone as assessed by measurements of sap flow through the trunk. However, as this approach is both labour-intensive and highly intrusive, heat balance gauges were adapted for use with lateral tree roots (cf. Section 2.5.4; Lott *et al.*, 1996) to estimate water uptake from within the crop rooting zone.

5.4.1 Contribution of lateral roots to total water uptake

Sap flow gauges attached to the trunk and all major lateral roots of individual trees (Plate 5.1c) were used to determine the fraction of total absorption that was extracted from the surface horizons by lateral roots. The trees were chosen to have a similar canopy size and hence potential for transpiration, but were growing in areas of differing soil depth (Table 5.3). Canopy size was calculated using the allometric approaches described previously (cf. Section 2.4.1; Lott *et al.*, 1998).

Sap flow through the trunk and the combined sap flow through all lateral roots exhibited distinct diurnal trends (Fig. 5.13), although Tree 1 exhibited an almost symmetrical response whereas the response of Tree 2 was asymmetrical. This suggests that Tree 1 was sufficiently well supplied with water for transpiration to track the diurnal pattern of solar radiation, and therefore resulted in a threefold difference in water use compared to

Plate 5.1 Excavation studies demonstrated the presence of limited numbers of large lateral roots (a; top) which extended for substantial distances through the surface horizons occupied by crop roots (b; bottom left). Heat balance gauges were used to measure water uptake by lateral roots from the crop rooting zone and total sap flow through the trunk (c; bottom right).

Table 5.3 Lateral root number, total cross-sectional area, mean daily transpiration and daily absorption, and fraction of total transpiration supplied by lateral roots in grevillea trees growing on soil of different depths.

Tree	Number of lateral roots	Total cross sectional area of lateral roots (cm^2)	Soil depth (cm)	Mean daily total transpiration (kg)	Daily absorption by all lateral roots (kg)	Fraction of transpiration supplied by lateral roots (%)
1	3	18.7	38	12.0	1.7	14
2	5	23.4	72	3.8	2.5	66

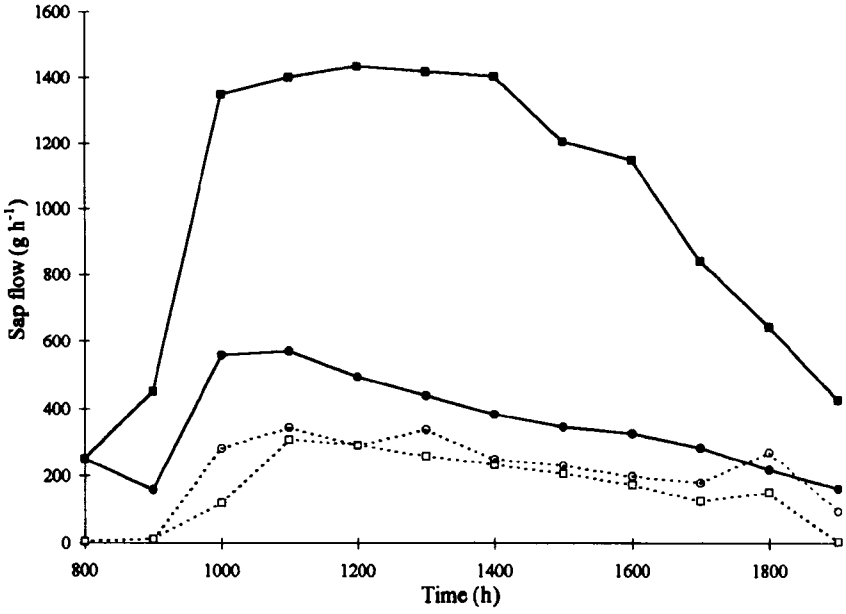

Figure 5.13 Typical diurnal timecourses for sap flow through the trunks and lateral roots of trees growing on soil of differing depth (cf. Table 5.3). Tree 1: solid squares, trunk; open squares, total for all lateral roots. Tree 2: solid circles, trunk; open circles, total for all lateral roots.

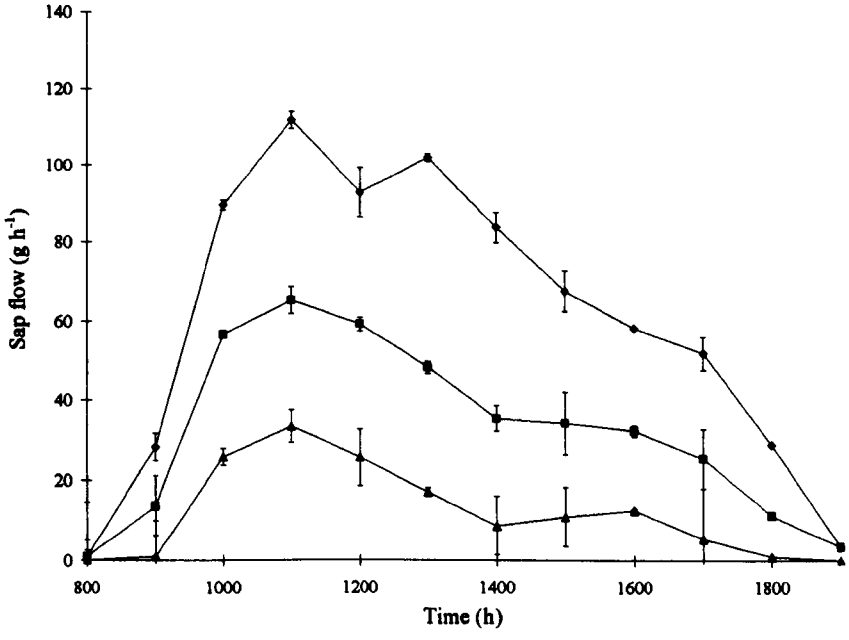

Figure 5.14 Diurnal timecourses of sap flow in lateral roots at distances of 50 (diamonds), 115 (squares) and 190 cm (triangles) from the trunks of grevillea trees. Double standard errors of the mean are shown.

Tree 2, despite growing on shallower soil. The mean volumetric soil moisture content of the surface horizons occupied by the lateral tree roots (approximately the top 60 cm of the profile) at this time was only 5 % (Wallace *et al.*, 1995), suggesting that Tree 1 was absorbing the majority of its water requirements from greater depths. Thus Tree 1 received only 14 % of its water supplies from the lateral roots as compared to 66 % in Tree 2 (Lott *et al.*, 1996). These observations strongly suggest that substantial quantities of water were absorbed by deeper roots penetrating into fissures in the underlying bedrock, a conclusion supported by the root excavation studies of Howard *et al.* (1997). The combined cross sectional area of the lateral roots was 25 % greater in Tree 2 than in Tree 1, reflecting the greater dependence of the former on water extracted from the surface horizons by lateral roots. These results demonstrate the existence of considerable functional and morphological variability between the root systems of trees of similar size.

Heat balance gauges were also used to measure sap flow through lateral roots at various distances from the trunk. Although sap flow through the lateral roots decreased sharply with increasing distance from the trees (Fig. 5.14), these well-established three-year-old trees nevertheless extracted substantial quantities of water from the crop rooting zone up to 190 cm from the trunk, at a time when the average volumetric soil moisture content in the upper 60 cm of the profile was 11 % (Lott *et al.*, 1996). This would result in large cumulative losses of water during the cropping season, particularly considering that extraction from the crop rooting zone by tree roots would be expected to be much greater during the rainy season when the soil frequently approaches field capacity (19 %). The importance of these competitive interactions between tree and crop roots is reflected by the marked reductions in the growth and productivity of maize growing within 2 m of the trees and consequent reductions in water use by maize (Figs. 5.9 and 5.10).

5.4.2 Compensation in water uptake

Heat balance gauges were attached to the trunk and one lateral root (Fig. 5.15a) of three trees of differing canopy size and to the trunks of paired control trees. After four days, all lateral roots except those with sap flow gauges attached were severed (Fig. 5.15b)

and five days later the root with the sap flow gauge attached was also severed (Fig. 5.15c). The effect of root pruning on sap flow through the trunks was assessed by comparison with the corresponding values for the paired unpruned control trees. Figure 5.16a shows diurnal timecourses of sap flow for three days during a twelve day experimental period when the lateral roots were successively severed. Sap flow through the trunk is expressed relative to the maximum recorded value over the measurement period (1000 h on 5 February, 1995) to account for differences in absolute water use between control and treatment trees prior to the experimental period. Sap flow through the instrumented lateral root is expressed as a fraction of the total sap flow for the same tree. At the time of these measurements during the dry season, mean soil moisture content was 7 % in the horizons occupied by lateral roots and 15-17 % at depth (Lott *et al.*, 1996).

Marked diurnal variation in water use was again apparent (Fig. 5.16a) and the control and treatment trees exhibited similar daily sap flow patterns prior to the first root pruning (Fig. 5.16b; Lott *et al.*, 1996). Excision of all lateral roots except for the one with the heat balance gauge attached (Fig. 5.15b) reduced total water use by about 20 % relative to control trees over a four day period (Figs. 5.16a and b). Sap flow through the remaining lateral root was only slightly increased, suggesting that this root was already operating near its maximum absorptive capacity for the prevailing soil conditions; this increase was insufficient to offset the reduced contribution by the other lateral roots and prevent a reduction in total water use. When the remaining lateral root was severed (Fig. 5.15c), sap flow through that root ceased and total water use showed a further small decrease (Figs. 5.16a and b). Total water use was nevertheless about 80 % of that in undisturbed control trees, supporting the evidence from Figure 5.13 (Tree 1) and root excavation experiments (Howard *et al.*, 1997) that grevillea may extract substantial quantities of water from below the crop rooting zone during the dry season.

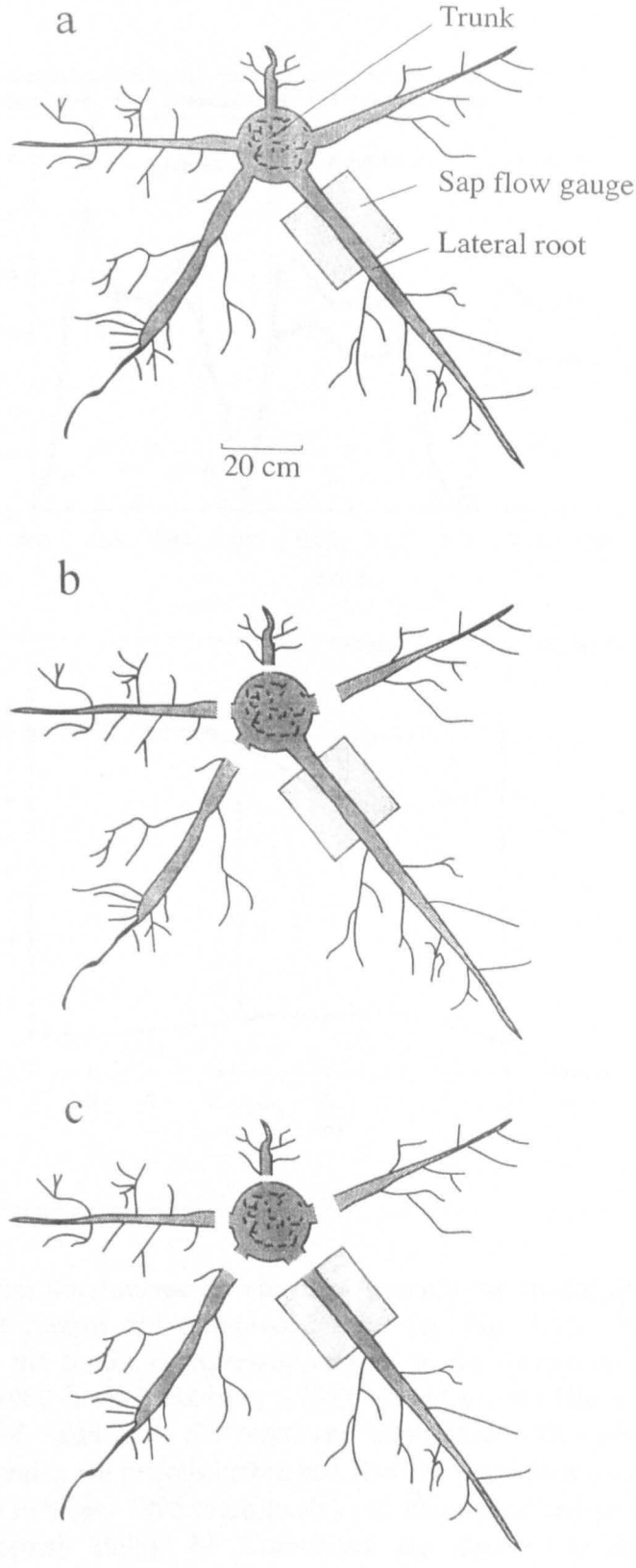

Figure 5.15 Sequence of lateral root pruning: a) five lateral roots identified and a heat balance gauge attached to one; b) four lateral roots severed adjacent to the trunk; and c) remaining lateral root with sap flow gauge severed.

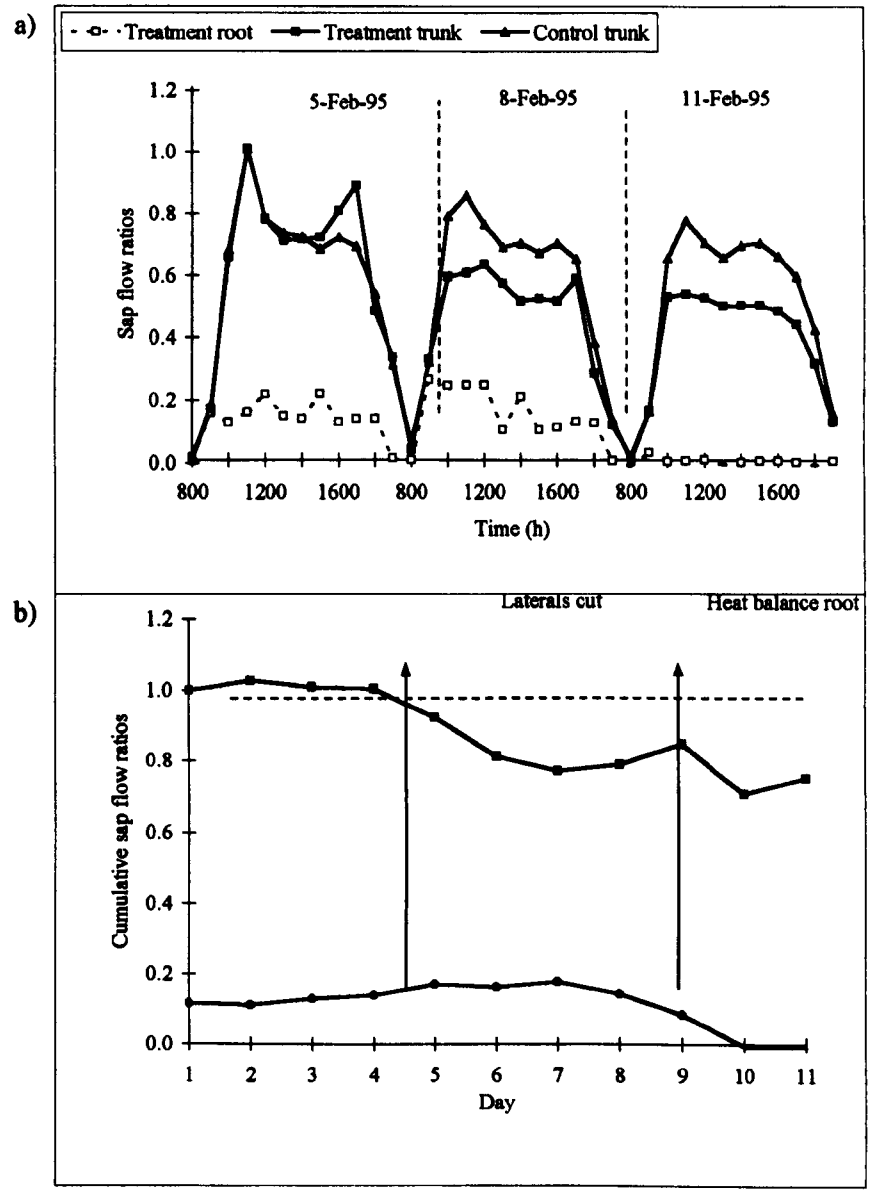

Figure 5.16 a) Diurnal timecourses for sap flow through the trunks and lateral roots of control and root-pruned trees (cf. Fig. 5.15). Sap flow through the trunks is expressed relative to the maximum recorded value (1000 h on 5 February 1995); values for the lateral root are expressed relative to the treatment trunk flow. The timecourses correspond to the periods before and after the first lateral root pruning (5 and 8 February 1995 respectively) and after the second root pruning (11 February 1995). b) Cumulative sap flow ratios during the experimental period (2-12 February 1995) for trunks (squares) and treatment lateral root (circles). Total daily water use by root-pruned trees is expressed relative to the unpruned controls; total daily sap flow for the treatment lateral root is expressed as a fraction of total water use by the tree. Vertical lines show the timing of root pruning (cf. Fig. 5.15).

CHAPTER 6

COMPARISON OF OUTPUT FROM HYPAR WITH OBSERVED MAIZE YIELDS IN CIRUS

This chapter describes initial steps taken to test the predictions provided by the integrated tree and crop growth model (HyPAR) developed by members of the Agroforestry Modelling Programme (cf. Section 1.5). Model output for growth, development and yield in maize grown as sole crops or as a component of agroforestry systems in semi-arid environments was tested against field observations. These modelling studies were approached from the viewpoint of potential non-expert end-users interested in testing model output against field data and establishing the extent of model parameterisation that is required for specific genotypes and sites. The results obtained demonstrate limitations in the functioning and mechanistic theory within the model which are required to be resolved in future research.

6.1 THE HYPAR MODEL

HyPAR is a mechanistically based agroforestry model created by combining the forest ecosystem model, Hybrid, with the dryland tropical crop model, PARCH. Brief overviews of HyPAR and its components are given below, whilst more detailed descriptions are provided by Lawson *et al.* (1996), Friend *et al.* (1997), Bradley and Crout (1994) and Bradley (1995).

Hybrid is an ecosystem model that simulates forest growth over large spatial and temporal scales and was originally written to represent the terrestrial biosphere in a total earth system model. In contrast, agroforestry and the underpinning research are generally carried out over small land areas and short time-scales. However, this should not pose major problems since Hybrid is based on the fundamental principles of energy cycling and resource capture, and so provides a suitable platform on which to build a mechanistic agroforestry model with a variety of end-user applications.

PARCH simulates the growth, development and yield of tropical C4 cereals, and takes particular account of the influence of solar radiation, soil water availability, atmospheric humidity and temperature under dryland conditions. Within the model, conversion coefficients describe the efficiency with which captured resources are converted to dry matter, and these are modified by a stress index to simulate the impact of water or temperature stress on crop growth. PARCH was originally calibrated for sorghum, for which its predictions agreed well with experimental data, accounting for 80 and 73 % respectively of the observed variation in yield and biomass at final harvest (Bradley, 1995).

HyPAR (Version 1) combines the crop resource capture and soil water movement routines of PARCH with the radiation interception, water use and annual biomass increment routines from Hybrid. The simulation cycles at daily intervals through the Hybrid routines for tree growth before passing to the crop growth routines. The trees are therefore considered to be the dominant component, with the crop environment being modified by the trees, although their impact on the crop is revised only at annual intervals since the trees 'grow' on a yearly timestep only.

6.2 INPUT FILES

6.2.1 Crop and cultivar-dependent parameters

As PARCH was initially parameterised for sorghum, many of the default values for the crop cultivar file are those for sorghum. The starting point for the present study was the improved cultivar parameter file for Katumani Composite B maize (KCB4; Table 6.1), which was defined at the PARCH modelling workshop held at Katumani, Machakos District, Kenya (Hess and Stevens, 1994). The objective of the workshop was to evaluate the suitability of PARCH for simulating the yields of the maize variety, Katumani Composite B (KCB), in the arid and semi-arid lands (ASAL) of Kenya; this cultivar was grown under comparable environmental conditions in the CIRUS programme. Parameterisation was based on the default values from PARCH-sorghum (standard.cul file), with modifications being made on the basis of output from CERES-Maize (calibrated for local conditions by Keating *et al.*, 1993), an

Table 6.1 Cultivar file (*KCB4*) for Katumani composite B maize (after Hess and Stevens, 1994).

Definition of parameter	Parameter code	Value	Units
Minimum partition of photosynthate to leaves during GS1 and GS2	minFL	0.1	proportion
Maximum partition of photosynthate to leaves during GS3	maxFL	0.8	proportion
Maximum partition of photosynthate to haulm during GS3	maxFH	0.1	proportion
Reserved for future expansion	null	0	-
Reserved for future expansion	null	0	-
Reserved for future expansion	null	0	-
Fraction of carbon to roots before stress adjustment	oFBG	0.25	proportion
Fraction of stem available for translocation	TransPot	0.3	proportion
Maximum fraction of stem available for translocation that can move per day	DayTransPot	0.1	fraction d^{-1}
Time for seed to use carbon supplies	germination	9	% C d^{-1}
Duration of plant juvenility - thin roots and leaves	Juvenile	11	d
Time from anthesis to grain set	GrainSetTime	17	d
Minimum time for grain filling	PartitionTime	44	d
Base cardinal temperature for growth	tb	8	°C
Maximum cardinal temperature for growth	tm	44	°C
Point where an increase in temperature has no more effect on growth	tbplateau	28	°C
Start of thermal denaturation - induces stress	tmplateau	34	°C
Reduction in thermal time accumulation as a result of stress prior to anthesis	GS1ttFactor	0.1	dimensionless
Increased maturity rate as a consequence of stress after anthesis	GS3ttFactor	0.03	dimensionless
Thermal time for Growth stage 1	GS1tt	223	°Cd
Thermal time for Growth stage 2	GS2tt	562	°Cd
Thermal time for Growth stage 3	GS3tt	474	°Cd
Tolerance of crop to water stress	STindex	3	dimensionless
Rate of recovery from stress	Recovery	0.5	% d^{-1}
Reduction in translocation rate as a consequence of stress	STransReduct	-0.5	dimensionless
Impact of stress on specific leaf area	SLAstress	0.7	dimensionless
Fraction of leaf area senescing per day as a consequence of stress	LeafStress	0.05	fraction d^{-1}
Increase in the fraction of carbon allocated to roots as a consequence of stress	RstressFBG	0.3	proportion
Maximum reduction of root extension rate as a consequence of stress	maxRstress	0.8	proportion
Maximum proportional reduction in light interception due to leaf rolling	lrollmax	0.4	proportion
Specific leaf area during Growth stage 1	SLA1	35	m^2 kg^{-1}
Specific leaf area during Growth stage 2	SLA2	25	m^2 kg^{-1}
Maximum leaf area for plants in a sparse canopy	MaxPlantArea	0.5	m^2
Rate of phenological death	LIFEC	0.5	dimensionless
Radiation conversion efficiency for Growth stage 1	Photosynth1	2.0	g MJ^{-1}
Radiation conversion efficiency for Growth stage 3	Photosynth3	1.7	g MJ^{-1}
Light extinction coefficient	k	0.65	dimensionless
Transpiration equivalent	qD	0.005	kg C kg^{-1} water kPa^{-1}
Conversion factor for grain number	GNC	2	dimensionless
Maximum grain weight	MaxGW	0.7	g
Minimum rooting depth	RDmin	20	mm
Maximum daily root extension rate	RRmax	25	mm d^{-1}
Maximum root length per unit volume	RLVmax	5	cm cm^{-3}
Roots are x-times thinner at germination	emRWLfactor	6	dimensionless
Roots are x-times more likely to grow downwards at germination	emRDfactor	4	dimensionless
Quantity of carbon per unit root length	RWLfactor	$1.5e^{-7}$	kg C cm^{-1}
Vertical roots are x-times thinner than average roots	FineRoot	12	dimensionless
Maximum water uptake rate	MaxUptakeRate	0.2	mm mm^{-1}
Root distribution half-depth function	Rdist	300	mm
Maximum rooting depth	maxRdepth	1200	mm
Permanent wilting point of plant	pWiltp	45	m
Fraction of soil saturation when plants experience waterlogging	WLsat	0.95	proportion
Factor to reduce the water uptake rate in response to waterlogging damage	WLdamage	2	dimensionless
Daily waterlogging recovery rate	WLrecover	1.1	fraction d^{-1}
Sensitivity to waterlogging of a portion of the root system	WLsuscept	5	dimensionless
Rate of population decline in response to waterlogging	WLdeath	0.1	fraction d^{-1}
Proportion of plant that was root when 'Ω' and 'Photosynth' were calculated	FractRoot	0	proportion

Table 6.2 Parameter file (*GREV97*) described for *Grevillea robusta* and based on the work of Friend *et al* (1997) and Mobbs and Cannell (1995).

Definition of parameter	Parameter code	Value	Units
PAR extinction coefficient	kpar	0.65	dimensionless
Short wave extinction coefficient	ksw	0.48	dimensionless
PAR reflection coefficient	rhop	0.05	dimensionless
Short wave reflection coefficient	rhos	0.20	dimensionless
Turnover rate of foliage	fturn	1.00	proportion yr^{-1}
Turnover rate of wood	wturn	0.01	proportion yr^{-1}
Turnover rate of fine roots	rturn	2.00	proportion yr^{-1}
Specific leaf area	sla	11.52	m^2 kg C^{-1}
Ratio of dbh to bark thickness	bark	0.033	m m^{-1}
Ratio between leaf area and sapwood area	lasa	4208.00	m^2 m^{-2}
Allometry a parameter for dbh to height	ah	33.918	m m^{-1}
Allometry b parameter for dbh to height	bh	0.464	m m^{-1}
Allometry c parameter for crown diameter	ch	0.45	m
Proportion of woody biomass below ground	stf	0.22	proportion
Biomass ratio for fine roots and foliage	rlratio	1.00	kg C^{-1} kg C^{-1}
Foliar nitrogen retranslocation coefficient	frcoeff	0.50	proportion
Fine root nitrogen retranslocation coefficient	rrcoeff	1.00	proportion
Mean wood and bark specific gravity	woodd	220.43	kg C m^{-3}
Tree form factor	formf	0.58	dimensionless
Ratio between C:N ratios of foliage and sapwood + bark	fsr	0.145	kg C kg N^{-1} (kg C kg N^{-1})$^{-1}$
Ratio between C:N ratios of foliage and fine roots	frr	0.86	kg C kg N^{-1} (kg C kg N^{-1})$^{-1}$
Proportion of sapwood alive	live	0.142	proportion
Maximum proportion of live sapwood used for C storage	storef	0.67	proportion
N uptake parameter	nupc	0.036	m^2 kg C^{-1} d^{-1}
Maximum leaf conductance to CO_2	ngr	1433.00	m s^{-1}
Cuticular conductance to CO_2	gmin	0.0000481	m s^{-1}
Proportion of foliar nitrogen bound in Rubisco	pruba	0.67	proportion
Proportion of foliar nitrogen bound in chlorophyll	nrc	9.13	proportion
Leaf characteristic dimension	d_leaf	0.04	m
Species vegetation type (1=grass;2=DECC;3=EVGR;4=D; 5=E)	ptype	5.00	dimensionless
Factor to allow for growth respiration	rgf	0.75	proportion
Factor for calculating minimum wood mass increment	wmf	0.10	proportion
Root weight per unit length	TreeRWL	1.5E-7	kg cm^{-1}
Factor for root distribution half depth	RD_to_hD	0.125	dimensionless
Factor for rooting depth from height	ht_to_RD	0.50	dimensionless

extensive literature survey, local knowledge and experimental research. A sensitivity analysis was also carried out for selected parameters including stress index, water use efficiency, the leaf stress factor, assimilate translocation, and grain number and weight.

The model proved capable of modelling maize yields in the ASAL, but tended to under-predict grain yield when stress occurred late in the growing season. This discrepancy was attributed to a lack of knowledge concerning the phenology, water use ratio and dry matter production of Katumani composite maize, the impact of late-season stress on assimilate translocation and the absence of reliable soil water and fertility data for calibrating the model. These deficiencies were addressed in the present study by using data collected within CIRUS to create a new cultivar parameter file, defined here as KCB97. Outputs obtained using both cultivar files were compared against the corresponding field data.

6.2.2 Tree parameters

The tree input parameters were based on the Eglo.par tree parameter file for eucalyptus (Mobbs and Cannell, 1995), which depended heavily on the broad-leaved, generalised ideotype described for Hybrid by Friend *et al.* (1997). This was possible because many parameters in Hybrid are fixed for all vegetation types, while others are constrained within narrow limits for broad or needle-leaved species. In addition, since much of the detailed physiological information required for trees is not available for individual species or genera, parameterisation has to rely heavily on a limited number of studies for a restricted number of species. Parameterisation of the input file for grevillea (GREV97.par; Table 6.2) was therefore heavily biased towards the broad-leaved ideotype described by Friend *et al.* (1997) and the EGLO.par input file for HyPAR (Mobbs *et al.*, 1995), and included only a limited number of parameters specific to grevillea, where these were available.

Table 6.3 General soil data required by HyPAR, parameterised for CIRUS.

Definition of parameter	Parameter code	Value	Units
Maximum soil depth	maxdepth	1100	mm
Use the nutrient subroutines?	Usenut	0	dimensionless
Soil nutrient content	Nutrient	0.05	$g\ g^{-1}$
Use the phosphorus subroutines?	UsePhos	0	dimensionless
C:P ratio of organic matter	OMCp	0.0	$g\ g^{-1}$
Proportion of total organic phosphorus that is stable	PhosStable	0.0	proportion
Proportion of total organic phosphorus that is labile	PhosLabile	0.0	proportion
Proportion of total organic phosphorus that is fertiliser	PhosFert	0.0	proportion
Proportion of total inorganic phosphorus that is active	PhosActIn	0.0	proportion
Proportion of total inorganic phosphorus that is stable	PhosStabIn	0.0	proportion
Empirical parameter to reduce root growth according to the strength of the soil	SSA	0	dimensionless
Empirical parameter to reduce root growth according to the strength of the soil	SSPR	2	dimensionless
Number of soil types (1-6)	NSoilTypes	5	dimensionless
Maximum soil water potential	swpmax	-0.01	MPa
Snowmelt coefficient	smeltc	0.0007	$m\ °C^{-1}\ d^{-1}$
Initial snow	snow	0.0	m

Table 6.4 Input files for depth of soil layers, initial water content and soil type for CIRUS at the start of the S94/95 season.

Width of layer (mm)	Water content (%)	Soil type
5	5	1
5	5	1
5	5	1
365	7	2
255	12	3
330	10	4
145	23	5

Table 6.5 Input files for depth of soil layers, initial water content and soil type for CIRUS at the start of the L95 season.

Width of layer (mm)	Water content (%)	Soil type
5	5	1
5	5	1
5	5	1
365	11	2
255	18	3
330	12	4
145	26	5

Table 6.6 PARCH hydrology model parameters as set up for CIRUS.

Definition of parameter	Parameter code	Value	Units
Infiltration rate scaling factor	Infilrate	0.6	dimensionless
Depth at which the number of cracks has declined by 50 %	CrackDist	500.0	mm
Proportion of rainfall which flows via soil cracks	CrackRate	0.0	proportion
Soil type specific scaling factor for drainage rate	DrainRate	0.0	dimensionless
Speed at which the model cycles through the hydology calculations (0.0 = OFF)	Speed	0.0	dimensionless

Table 6.7 Soil physical characteristics for the five soil types defined for the CIRUS site including clay, sand and silt fractions, bulk density, permanent wilting point, field capacity, field saturation and saturated conductivity.

Definition of parameter	Parameter code	Units	Soil type 1	Soil type 2	Soil type 3	Soil type 4	Soil type 5
Clay fraction	fclay	%	0.355	0.425	0.425	0.365	0.235
Silt fraction	fsilt	%	0.090	0.090	0.090	0.090	0.140
Sand fraction	fsand	%	0.555	0.485	0.485	0.545	0.625
Bulk density	bulkden	$g\ cm^{-3}$	1.193	1.207	1.298	1.456	1.440
Permanent wilting point	SminAW	%	13.000	15.500	12.100	10.500	10.100
Field capacity	SFCap	%	23.100	27.100	25.000	21.920	21.920
Soil saturation capacity	Ssaturated	%	40.000	42.760	40.000	35.070	35.070
Saturated conductivity	Sksat	$mm\ s^{-1}$	0.00668	0.00399	0.00149	0.00639	0.00856

Table 6.8 Yields and growth stage durations observed in CIRUS compared with output from HyPAR after the first validation. Results are shown for maize grown as a sole crop (Cg) or in the dispersed agroforestry (CTd) treatment.

	S94/95				L95			
	Observed		First Validation		Observed		First Validation	
	Cg	CTd	Cg	CTd	Cg	CTd	Cg	CTd
Grain yield ($t\ ha^{-1}$)	2.06	0.82	0.62	0.04	1.14	0.14	0.74	0.01
Total dry matter ($t\ ha^{-1}$)	3.13	1.48	2.82	0.21	2.43	0.31	3.92	2.07
Duration of growth stage 1 (d)	20	21	18	18	20	30	17	17
Duration of growth stage 2 (d)	33	35	33	48	29	40	44	47
Duration of growth stage 3 (d)	70	66	80	39	63	32	40	41
Duration of growing season (d)	123	122	131	105	112	102	101	105
Seasonal rainfall (mm)	635	635	635	635	311	311	311	311

6.2.3 Soil and soil water characteristics

The data required to parameterise soil physical characteristics were drawn predominantly from the Institute of Hydrology's extensive dataset for CIRUS (courtesy Dr. N. Jackson; cf. Tables 6.3-6.7). Soil depth varied greatly across the site but, after extensive analysis of the relevant survey data (cf. Section 2.3), a depth of 1100 mm was selected as providing a representative mean for all HyPAR simulations. As nutrient availability was non-limiting in CIRUS (cf. Section 2.3), the nutrient parameters within the model were either switched off or set to non-limiting values. Initial soil water content at each defined depth was calculated from neutron probe and TDR measurements made immediately before each growing season used for simulation analysis (Tables 6.4 and 6.5). The infiltration rate parameter in HyPAR is set on a scale of 0-1 depending on the soil type involved, and in the present study was initially set at 0.6 (Table 6.6) to represent the moderately freely draining sandy loam at the CIRUS site (Jackson, pers. comm.). The soil crack rate parameter in the model takes account of macropores present within the soil, but since these were largely absent in CIRUS due to the high sand content of the soil and its low earthworm activity, this parameter was set to zero. The drain rate value was also set to zero since drainage through the bedrock was extremely slow (Jackson, pers. comm.). Crout (pers. comm.) advised that several thin soil layers should be specified at the soil surface to allow the hydrology model within PARCH to provide more realistic simulations of evaporation and infiltration; three 5 mm thick layers of the same soil type were therefore stipulated. Five soil categories (soil types 1 to 5) were identified within the soil profile in CIRUS, and soil texture (Jackson, unpublished), soil water release curves, and bulk and particle densities (Wallace *et al.*, 1995) were defined for each (Table 6.7). However, data describing the saturated conductivity of the soil (Ksat) were not available since analysis of the relevant data was incomplete prior to the modelling study reported here. Ksat was therefore calculated using the method adopted in PARCH, which is based on the work of Campbell (1974, 1985) and Gregson *et al.* (1987) and is comparable to that used in the SWEAT model (Daamen and Simmonds, 1995). Soil characteristics were similar to those at a nearby site where the sand, silt and clay fractions were known (Kilewe and Ulsaker, 1984).

6.2.4 Meteorological data

HyPAR is capable of generating daily weather patterns from monthly mean values to allow simulations to be run when suitable local values are not available. As appropriate meteorological data were available for CIRUS, recorded by the automatic weather station located above the tree canopy (cf. Section 2.1), these were used to drive the climate files for the HyPAR simulations (Fig. 6.1). Two consecutive seasons in which seasonal rainfall and its distribution differed greatly were simulated, the 1994/95 short growing season (S94/95) and 1995 long growing season (L95). Seasonal total rainfall during S94/95 (628 mm) was much above average (414 mm), although an extended dry period occurred during the first 17 days after sowing (DAS). Rainfall in L95 (302 mm) was near average (359 mm), but occurred mainly during the early part of the season, causing the crop to be severely water-limited later in the season. The initial soil water content at depth was also greater during L95 than S94/95, increasing still further the quantity of water available to support early-season growth.

HyPAR runs on an annual cycle, with model output being downloaded on the last day of the simulation year. HyPAR also allows only one crop to be grown within each simulation cycle. However, there are two growing seasons in Eastern Kenya, extending between October-February and March-July (short and long growing seasons respectively) and therefore the simulation was run twice to obtain data for crop performance in each season. In addition, since HyPAR can only download output on the final day of the simulation, on 31 December which is midway through the short growing season, separate meteorological data files were created so that the start of each simulation cycle corresponded with the beginning of the appropriate cropping season. Thus, to produce simulations for the short growing season, the meteorological data files were set up so that October replaced January as the first month of the simulation year, while March was used as the first month of the simulation cycle for the long growing season.

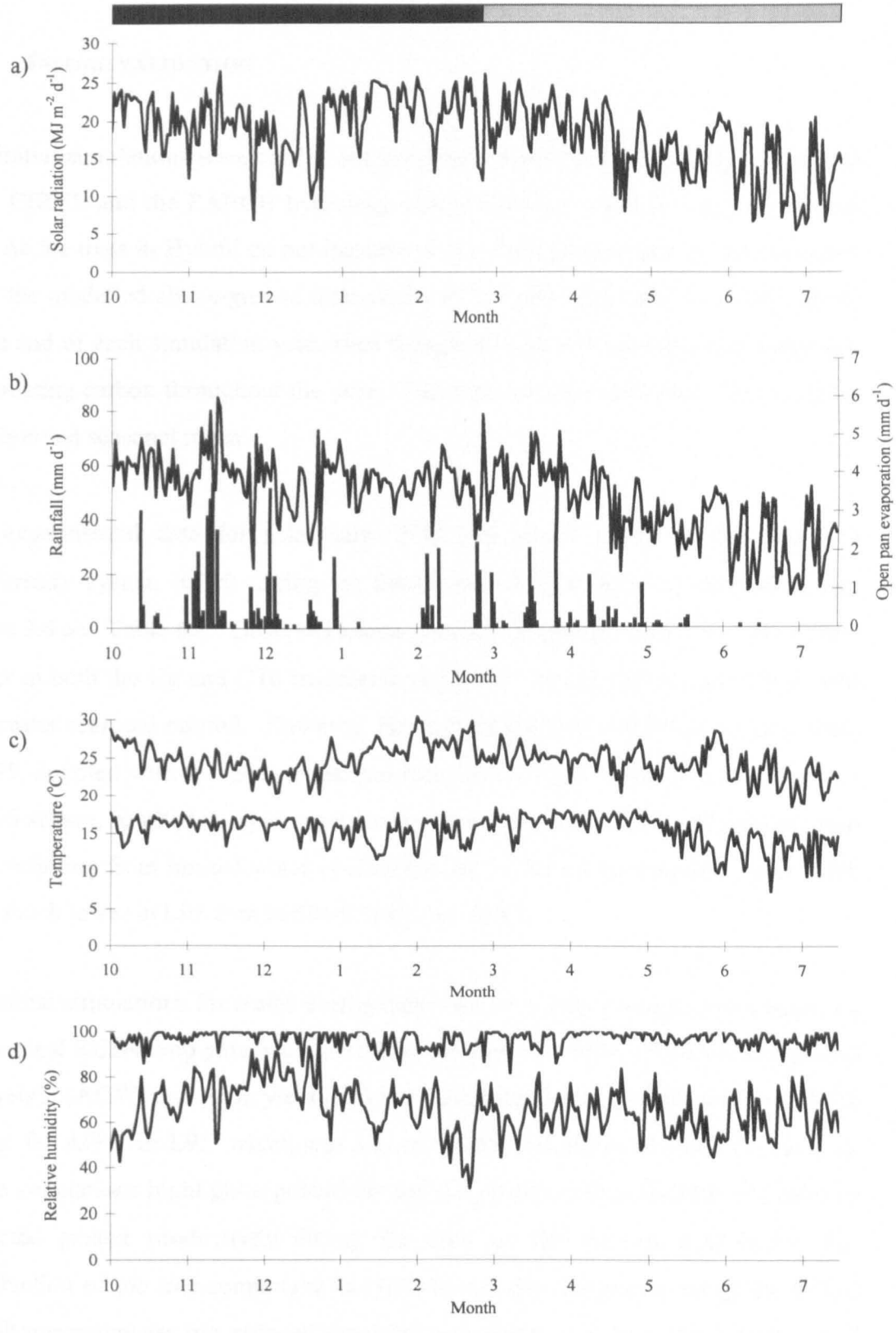

Figure 6.1 Timecourses for a) total daily shortwave radiation, b) daily rainfall (columns) and daily open pan evaporation (line), c) maximum (upper line) and minimum (lower line) air temperatures, and d) relative humidity at 0700 (upper line) and 1400 (lower line), used as climatic data in simulations with HyPAR. Horizontal bars represent seasons; black, short growing season 1994/95 (Oct-Feb) and grey, long growing season 1995 (Mar-Jul).

6.3 INITIAL VALIDATION

The initial simulations were carried out using the appropriate meteorological datasets from CIRUS and the PARCH hydrology model with the nutrient routines switched off. As the trees in Hybrid do not increase in size during the course of the simulated year, the modelled above-ground interactions do not alter since the trees only 'grow' at the end of each simulation year, even though they have been absorbing water and assimilating carbon throughout the year. Tree size was therefore set in the model at the observed seasonal mean.

The experimental data for sole maize (Cg) and maize grown in the dispersed agroforestry system (CTd) during the S94/95 and L95 seasons are summarised in Figure 3.6 and Table 6.8. Observed above-ground biomass and yields for maize were higher in both the Cg and CTd treatments in S94/95 than in L95, in agreement with the greater seasonal rainfall. However, the high intensity of rainfall at the beginning of L95, coupled with the greater residual soil water content from the preceding wet S94/95 season, resulted in rapid vegetative growth. The subsequent reduction of grain yield resulting from limited water availability late in the season caused harvest index to be much lower in L95 than in S94/95 (0.47 *vs.* 0.66).

The initial simulations for maize during these two contrasting seasons were based on the original KCB4 crop parameter file (Hess and Stevens, 1994). Total above-ground dry weight (AGW) and grain yield (Yg) were consistently underestimated by HyPAR except for AGW in L95, which was almost double the observed value (Table 6.8). These simulations highlight a potentially serious problem since HyPAR consistently predicted greater productivity during the drier of the seasons examined. The introduction of the tree component of HyPAR into the simulation, using the EGLO default tree parameter file, reduced simulated crop yields relative to the corresponding sole crop values (Table 6.8) but retained the anomaly that productivity was higher during the drier L95 season. When compared to the observed yields, simulated yields in the agroforestry system were underestimated during S94/95 but overestimated during L95, particularly for AGW. A sensitivity analysis was therefore carried out to

identify the elements of HyPAR responsible for these discrepancies between observed and simulated yields.

6.4 SENSITIVITY ANALYSIS

Sensitivity analyses of key sub-models and routines within HyPAR was achieved by systematically altering parameters and comparing output with observed yields. This may assist in refining the model and reducing the number of input variables required to suit the relatively limited datasets typically available to extensionists. These analyses concentrated on parameters which were either identified by Hess and Stevens (1994) as requiring further validation, were acknowledged to be based on poor quality information, or were involved with the water balance sub-routines within the model. It was felt that the latter might provide information concerning the possible origin of the inconsistency between predicted yields for the wet and dry seasons highlighted above. The sensitivity analyses have been grouped into sections concentrating either on soil hydrology and water relations or on cultivar-specific parameters.

6.4.1 Soil hydrology and water relations

Extensive sensitivity analyses for parameters related to the water relations sub-routines in the model (atmospheric humidity, initial soil water content and rainfall distribution) suggested that the unrealistically low simulated yields for the S94/95 season resulted from the 17 day dry period at the beginning of the season. Thus simulated yields could be increased dramatically by replacing the initial soil water content values with the higher values recorded for L95; this procedure increased simulated grain yield (Yg) by 135 % and total dry weight (AGW) by 70 %. Further analyses in which soil moisture content within the model was successively increased at each soil depth by 6 mm (the maximum difference between L95 and S94/95) showed that the greatest impact occurred when the moisture content of the 380-965 mm horizons was increased, but that there was no effect of increasing soil moisture in the 15-380 mm layers. These results indicate that simulated yields were limited primarily by a lack of soil water at depth within the profile. Artificially adding rainfall during the first 17 DAS, when only a single rainfall event of 10 mm occurred

which therefore resulted in periods of 4 and 10 days without rain, had a similar effect on simulated yields, although the size of the response depended on the distribution of rainfall. For example, 40 mm of rainfall supplied midway through either dry period was less effective in increasing yield than 10 mm added four times at regular intervals during each dry period, probably because the runoff predicted by the model declined as the intensity of rainfall decreased.

The version of the PARCH hydrology model incorporated into HyPAR provides little opportunity to vary the proportion of rainfall that is partitioned to runoff. Parameters which affect infiltration are also those which describe soil physical characteristics, such as the presence/absence of macropores and soil type. The more recent v3.00 version of PARCH includes a user-defined soil surface water-holding capacity which is a function of slope, surface roughness and saturated conductivity; any rainfall above this water-holding capacity may be lost as runoff. In addition, PARCH v3.00 allows adjacent experimental areas to be modelled so that runoff from one becomes run-on to another, where it can potentially infiltrate depending on soil water storage capacity, the rate of surface water movement and the depth of standing soil water (the puddle). HyPAR may simulate crop yields more effectively if these PARCH v3.00 sub-routines were included within the PARCH framework of the model.

The quantity of rainfall lost as runoff could be reduced by c. 10 % in both S94/95 and L95 by setting the infiltration rate parameter in HyPAR to 1 (maximum on a scale of 0-1). This resulted in simulated runoff greatly exceeding the observed in S94/95 (46 *vs.* 33 %), but being less than the observed in L95 (33 *vs.* 38 %). However, an infiltration rate of 1 represents a very freely draining sandy soil which is an unrealistic description of the characteristics of the sandy clay loam present at the CIRUS site. The sensitivity of model output to changes in the infiltration parameter is illustrated in Figure 6.2 for both seasons examined.

In addition to infiltration rate, two further parameters within the PARCH hydrology model, CrackDist and CrackRate, could potentially alter runoff. These parameters refer to the presence of soil macropores which are important in transferring water to

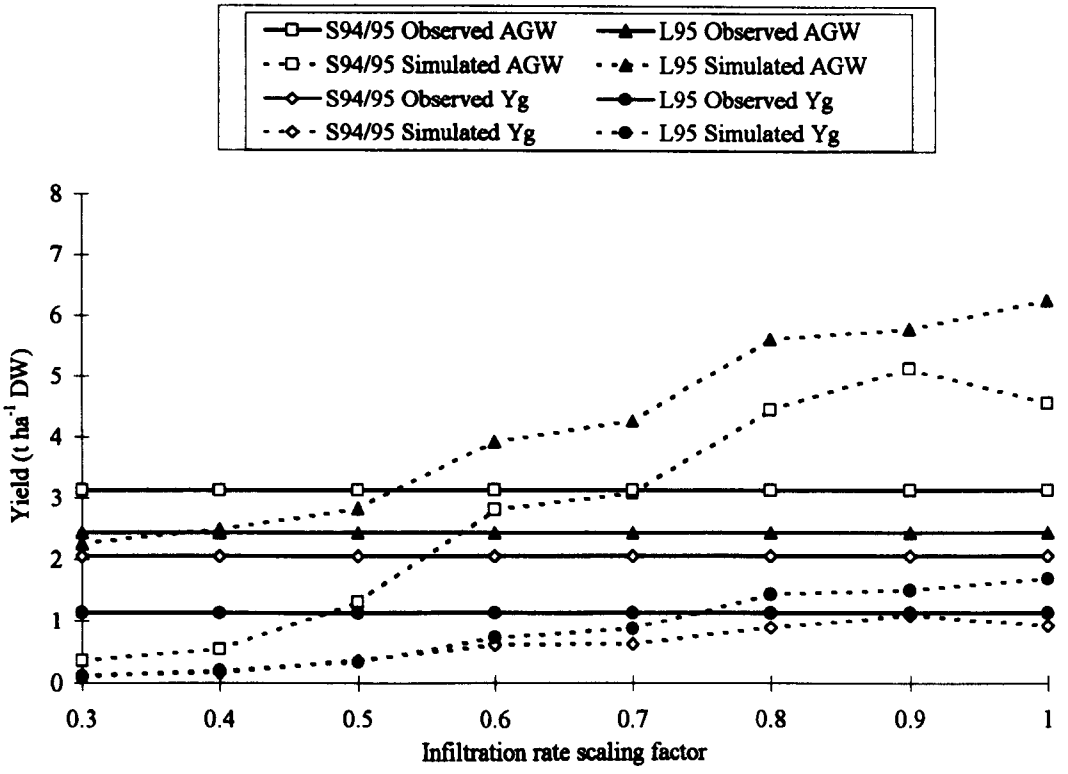

Figure 6.2 Effect of changing the infiltration rate scaling factor in HyPAR on simulated grain yield (Yg) and biomass (AGW) of KCB4 maize during the S94/95 and L95 seasons. Solid lines represent the observed yields in CIRUS.

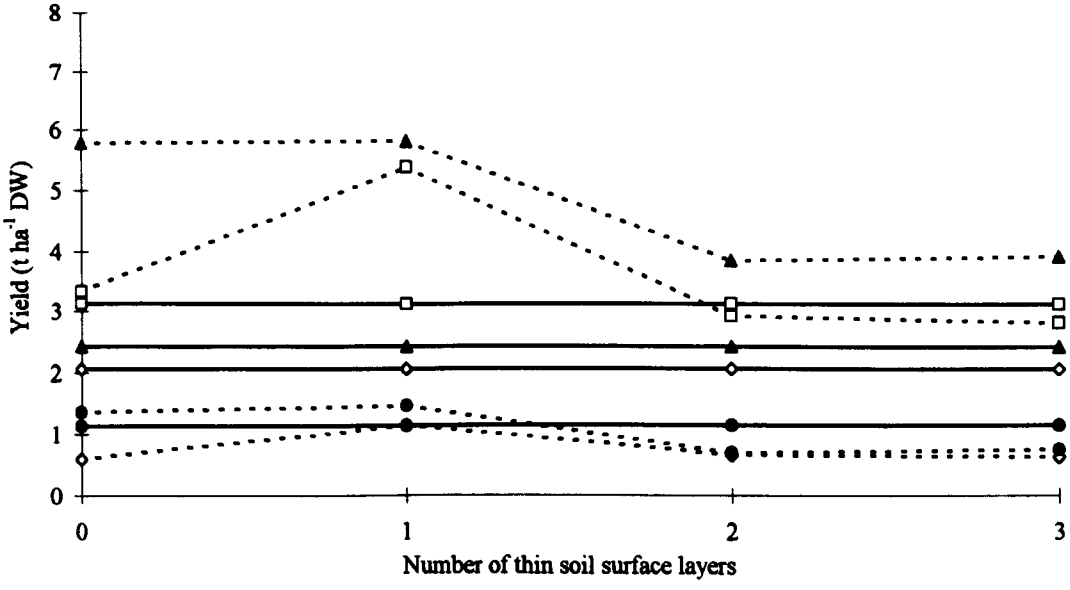

Figure 6.3 Effect of changing the number of thin (5 mm) soil surface layers in HyPAR on simulated grain yield (Yg) and biomass (AGW) of KCB4 maize during the S94/95 and L95 seasons. Solid lines represent the observed yields in CIRUS.

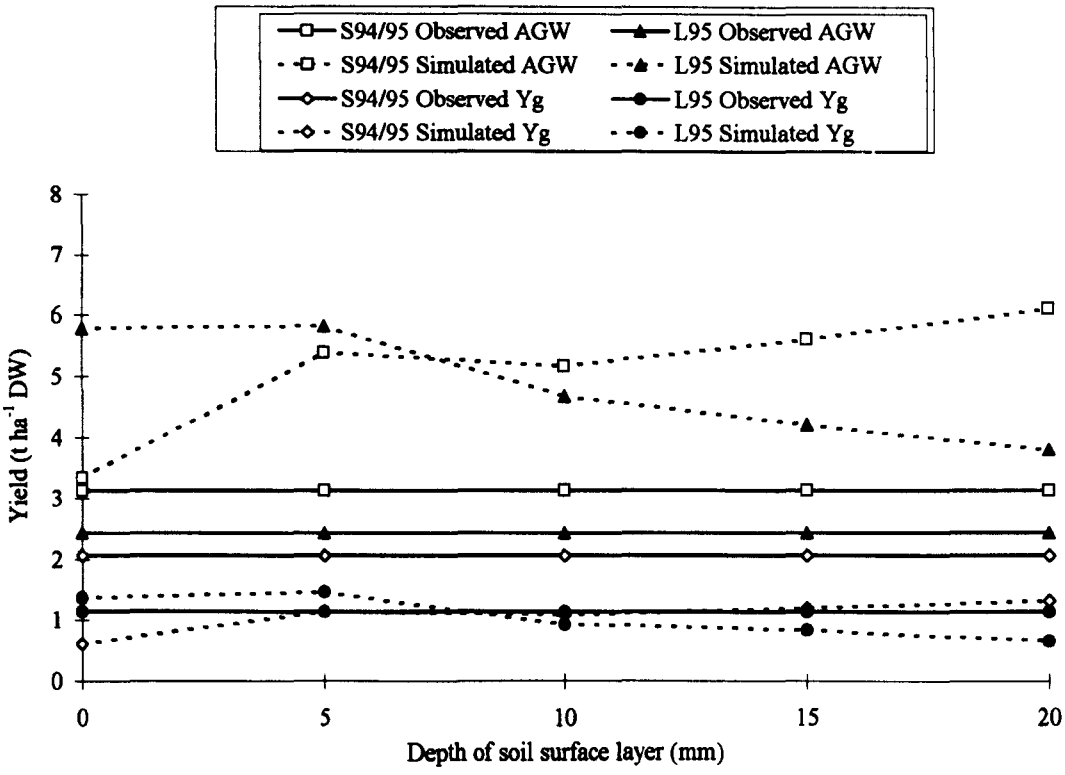

Figure 6.4 Effect of changing the depth of a single thin soil surface layer in HyPAR on simulated grain yield (Yg) and biomass (AGW) of KCB4 maize during the S94/95 and L95 seasons. Solid lines represent the observed yields in CIRUS.

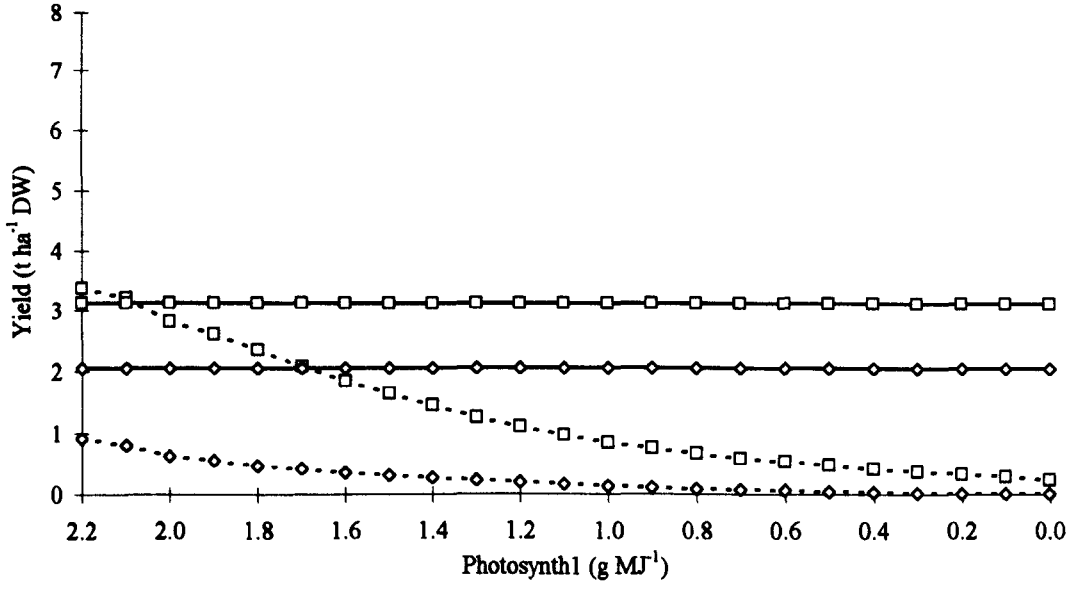

Figure 6.5 Effect of changing the Photosynth1 (radiation use efficiency) factor in HyPAR on simulated grain yield (Yg) and biomass (AGW) of KCB4 maize during the S94/95 season. Solid lines represent the observed yields in CIRUS.

depth in the soil profile. However, manipulation of these parameters had no effect on the predicted values for runoff or yield in either season in this version of HyPAR.

A preliminary version of an alternative hydrology model developed by members of the DFID Agroforestry Modelling Programme, which allows the Rawls-Brakensiek pedo-transfer function to be used, was made available for the current study (courtesy J. Arah and M. Hodnett); this model allows complete infiltration of rainfall, thereby removing the runoff term. Setting the parameters within this hydrology model to values equivalent to the PARCH hydrology model ensured that the only apparent difference between simulations using both models was the absence of runoff in the simulations. Alternative meteorological files were then set up for each season so that the quantities of rainfall were pre-adjusted to account for the observed loss to runoff. This was achieved by calculating the proportion of rainfall lost to runoff using the equation of Wallace *et al.* (1995):

$$\text{Runoff} = (\text{rainfall} \times 0.254) - 1.835 \qquad \text{Equation 6.1}$$

which included a threshold rainfall value of 7 mm below which no runoff occurred. Model output was therefore directly comparable with the field data in terms of the impact of runoff since the proportion of rainfall entering the soil corresponded to that observed. However, as the simulated yields were lower during both seasons than those predicted using the runoff sub-routines of the PARCH hydrology model (S94/95; Yg = 0.45 t ha^{-1}, AGW = 1.389 t ha^{-1}, L95; Yg = 0.20 t ha^{-1}, AGW = 2.631 t ha^{-1}), this simulation provided poorer accuracy. Further analysis revealed that the inclusion of cracks within the simulation, particularly those extending throughout the profile (50 % total crack density at 1 m depth), improved yields dramatically during both seasons (S94/95; Yg = 2.21 t ha^{-1}, AGW = 7.48 t ha^{-1}, L95; Yg = 1.67 t ha^{-1}, AGW = 6.35 t ha^{-1}). This observation supports the conclusion drawn from the initial analysis of soil water content that modelled crop yields responded best to increased water content at depth in the soil profile rather than in the top 40 cm. Thus, yield suppression was not caused by poor simulation of runoff, but probably originated from the sub-routines controlling infiltration to depth. Further work is clearly required to improve the hydrology sub-routines within PARCH.

As indicated earlier, three thin soil layers were specified at the soil surface to enable the PARCH hydrology model to provide more realistic simulations of evaporation and infiltration (Crout, pers. comm.). Figure 6.3 illustrates the effect of these layers on runoff and yield predictions for both seasons, while the effect of varying the depth of a single soil surface layer between 0-20 mm is shown in Figure 6.4.

Since site-specific data for saturated conductivity (Ksat) were not available and therefore had to be estimated using PARCH, the sensitivity of model output to changes in this parameter was assessed. Systematic alteration of Ksat around the values calculated by PARCH had no significant effect on simulated yield in either season, suggesting that the absence of reliable data for this parameter does not seriously influence model output.

The higher mean relative humidity in S94/95 than in L95 would have been expected to reduce transpirational demand, thereby favouring crop growth. Indeed, the calculation of daily transpiration (Q, mm d^{-1}) made by HyPAR using:

$$Q = G \times \frac{D}{W} \qquad \text{Equation 6.2,}$$

where G represents the daily growth rate (g m^{-2} land area d^{-1}), D denotes saturation deficit (kPa) and W is the crop transpirational equivalent or dry matter/water use ratio (g DW mm^{-1} water kPa^{-1}), stresses the importance of atmospheric moisture content by assigning saturation deficit to the denominator. Growth rates are calculated according to the availability of light (G_L), water (G_w) and nutrients (G_N), and G is determined by whichever of these is lowest. Since water is generally the most important limiting resource under semi-arid conditions, G is determined primarily by the water-limited growth factor (G_w) where:

$$G_w = X_{max} \times \frac{qD}{D} \qquad \text{Equation 6.3,}$$

and X_{max} represents the maximum quantity of water the root system can supply (mm d^{-1}). The anomaly that simulated yields were lower in the wetter and more humid S94/95 season than in the drier L95 season is difficult to explain since analysis of the sensitivity of model output to variation in the input values for relative humidity revealed that simulated yields responded as expected, being inversely related to saturation deficit. Thus the lower simulated yields for S94/95 could not be attributed to poor interpretation of the impact of atmospheric humidity on transpiration within the mechanistic framework of the model, but were most probably the result of difficulties with the soil water sub-routines, as concluded earlier.

6.4.2 Cultivar specific parameters

The model is extremely sensitive to variation in the values for Photosynth1 and Photosynth3, which respectively represent the radiation use efficiencies (RUE) of maize up to flowering and during grain filling. Hess and Stevens (1994) set these at 2.0 and 1.7 g MJ^{-1} in KCB4, although both values are high relative to those reported previously for maize grown in semi-arid environments. Thus, Carberry *et al.* (1989) allocated values of 1.70 and 1.07 g MJ^{-1} when calibrating CERES-maize for semi-arid environments, while Muchow and Davis (1988) set values of 1.6 and 1.4 g MJ^{-1}. Squire (1990) suggested that RUE may vary when C4 cereals are grown on drying soil under large saturation deficits, and his subsequent analysis suggests that RUE values for maize in CIRUS would range between 1.4-1.7 g MJ^{-1} in view of the prevailing relatively dry environment, high saturation deficits and relatively low temperatures. Figures 6.5 and 6.6 illustrate the impact of varying Photosynth1 and Photosynth3 on simulated yields during the relatively wet S94/95 season. Predicted grain yield (Yg) never matched the observed values during separate simulations using high values for either Photosynth1 or Photosynth3. Even when Photosynth1 and Photosynth3 were both set to the maximum physiologically acceptable value of 2.2 g MJ^{-1}, the simulated value for Yg was only half that actually observed.

Maximum individual grain weight (GWmax) was varied during the initial validation of PARCH (Hess and Stevens, 1994) between 0.4 g, the highest reported value in the literature, and 0.7 g. These workers also simultaneously lowered the grain number

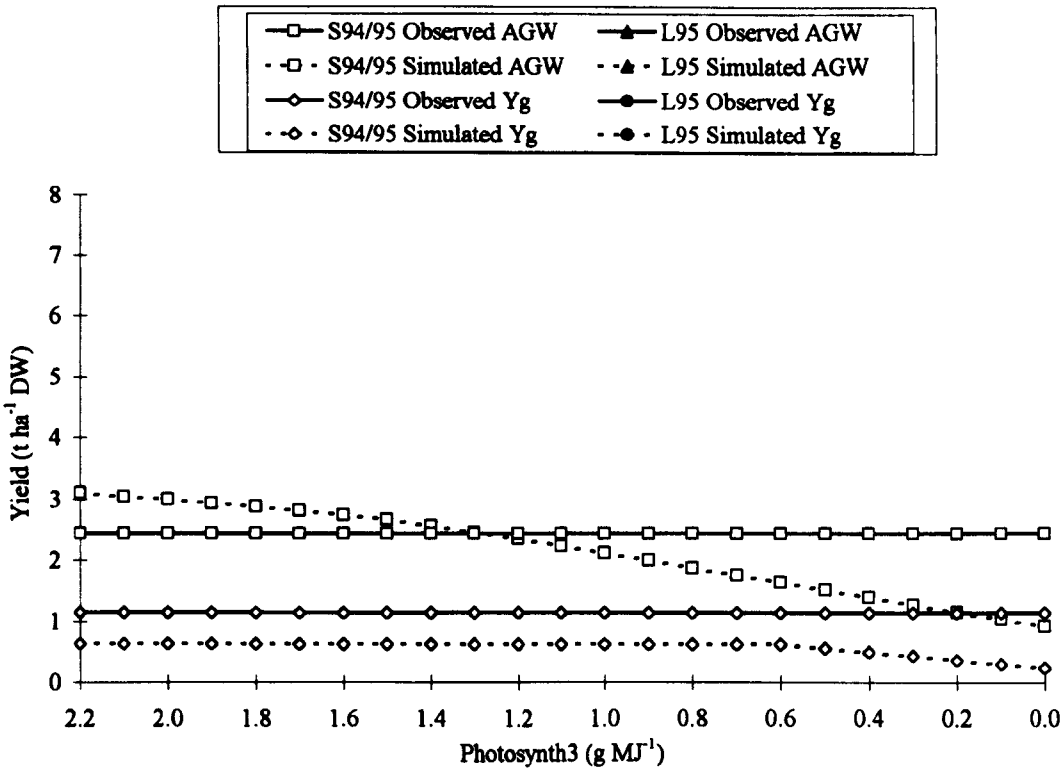

Figure 6.6 Effect of changing the Photosynth3 (radiation use efficiency) factor in HyPAR on simulated grain yield (Yg) and biomass (AGW) of KCB4 maize during the S94/95 season. Solid lines represent the observed yields in CIRUS.

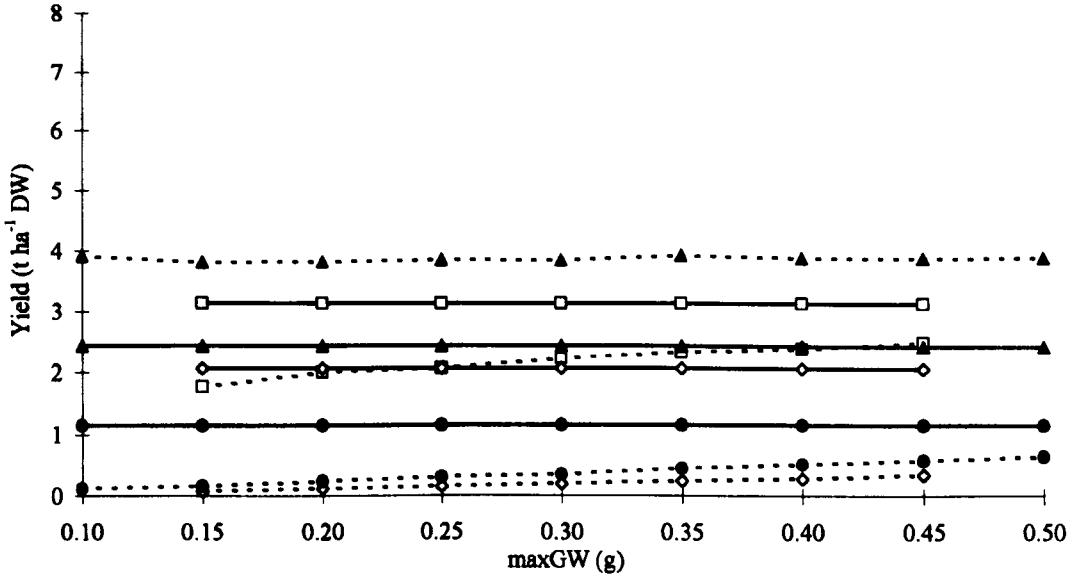

Figure 6.7 Effect of altering the maximum grain weight parameter in HyPAR on simulated grain yield (Yg) and biomass (AGW) of KCB4 maize during the S94/95 and L95 seasons. Solid lines represent the observed yields in CIRUS.

conversion factor (GNC) from 18 to 2; GNC is multiplied by the dry matter increment during growth stage 2 (GS2) to calculate the number of grain sites that are set in HyPAR simulations. These modifications were intended to increase simulated grain yield (Yg) so that the harvest indices were brought closer to the observed values, although there is no physiological justification for assuming such high maximum grain weights. This view was supported by the field measurements in CIRUS, which provided a maximum grain dry weight of 0.41 g and a mean of 0.27 g. The occurrence of relatively low simulated Yg values is more likely to have resulted from limitations on the number of grains set or the availability of carbohydrate to partition to the developing grain. Increasing the GNC factor, and hence grain number, to the maximum value within the range given in the PARCH manual (50) and setting GWmax to the maximum reported value of 0.4 g still produced predicted yields which were lower than observed, although the harvest indices were much closer to those recorded (S94/95, observed 0.66, simulated 0.47; L95, observed 0.47, simulated 0.61). Maximum grain weights reported in the literature range between c. 0.2-0.4 g, e.g. 0.27-0.40 g, (Early *et al.*, 1967); 0.28-0.32 g, (Duncan *et al.*, 1973); 0.20-0.40 g; (Norman *et al.*, 1984); 0.27 g, (Jones *et al.*, 1985); 0.28 g, (Muchow, 1990); 0.33-0.41 g, (Cooper and Law, 1978). Sensitivity analysis of the effect of varying GWmax within this range produced a greater than two-fold difference in Yg in both seasons (Fig. 6.7), suggesting sink limitation. Interestingly, simulated AGW for L95 was unaffected by GWmax, whilst that for S94/95 showed a c. 25 % increase over the 0.2-0.4 g range, suggesting that the increase in simulated Yg during L95 resulted from increased translocation from the vegetative organs, whilst the provision of a larger sink by increasing grain number during the simulations for S94/95 arose from increased resource capture and allocation to both the vegetative and reproductive organs. The PARCH manual (v2.01) suggests that GNC should be set within the range 15-50. However, Figure 6.8 shows that Yg was insensitive to decreases in GNC within this range during S94/95 and was unaffected until a value of 25 was reached during L95, below which Yg decreased by c. 40 %. The most dramatic effect on Yg occurred when GNC was reduced below 5; since the default KCB4 cultivar file sets GNC at 2, grain yield would be seriously sink-limited within the model. It is therefore suggested that, in the absence of reliable information concerning appropriate

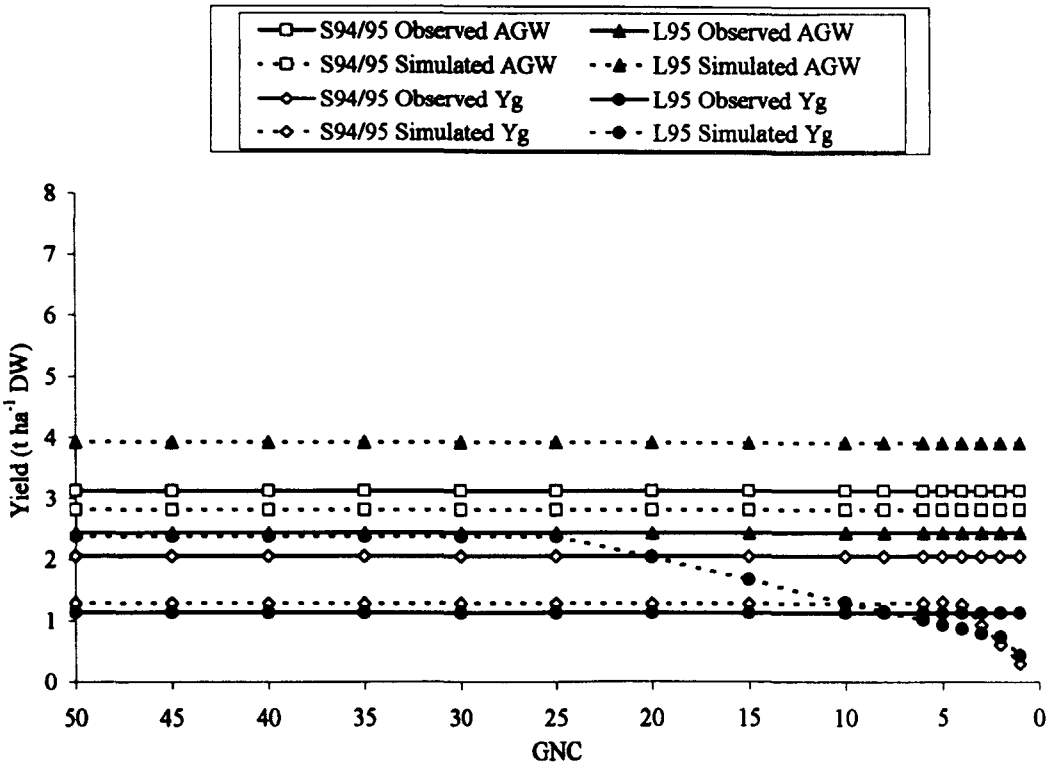

Figure 6.8 Effect of altering the GNC parameter (used in the calculation of grain number) in HyPAR on simulated grain yield (Yg) and biomass (AGW) of KCB4 maize during the S94/95 and L95 seasons. Solid lines represent the observed yields in CIRUS.

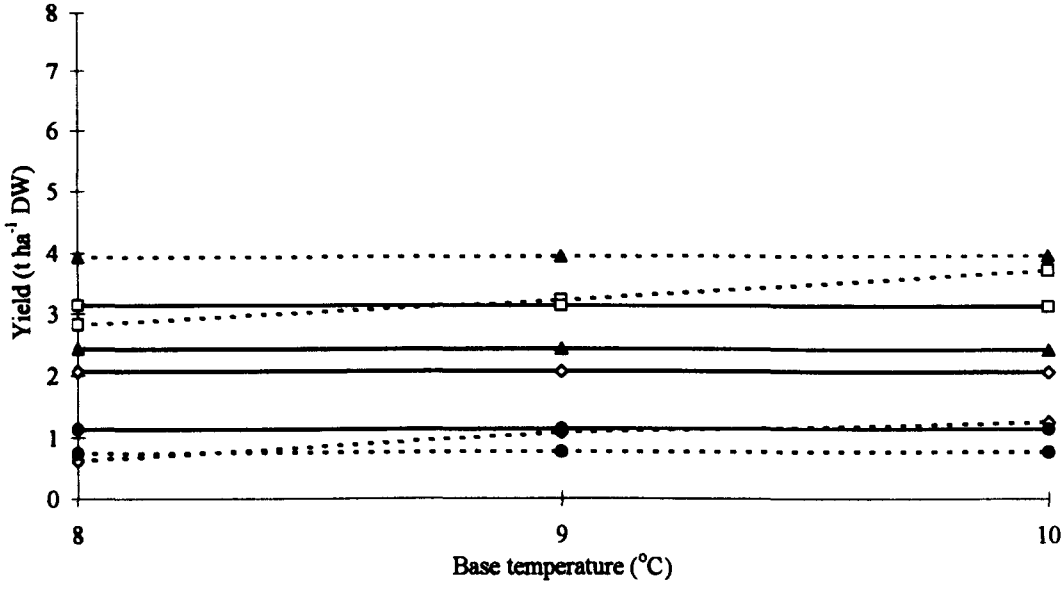

Figure 6.9 Effect of altering base temperature in HyPAR on simulated grain yield (Yg) and biomass (AGW) of KCB4 maize during the S94/95 and L95 seasons. Solid lines represent the observed yields in CIRUS.

values for GNC, this factor should be set to non-limiting levels (i.e. >25) so that grain number is limited only by the dry matter increase during GS2.

Hess and Stevens (1994) ascribed the relatively low grain yields predicted by PARCH to limitations on dry matter production imposed by severe late-season water stress. They therefore assigned the Transpot scaling factor a value of 0.3 (30 % *vs.* the default of 20 %) so that a larger proportion of the assimilates produced by the stem and leaves was translocated to the developing grain to supplement declining supplies from current photosynthesis. A 30 % translocation factor from stems and leaves to the grain is high, but within the range quoted by Ritchie (1991). Hess and Stevens also made the STransReduct factor a negative quantity (-0.5), even though this term is defined as a 0-1 scaling factor within the model, so that translocation increased as the stress became more severe. This adjustment is physiologically acceptable to a limited degree since short-term mild to medium stress may increase translocation, whereas more prolonged or severe stress inhibits water transport, thereby restricting translocation (Jordan, 1983). However, analysis of model sensitivity to variation in STransReduct based on the current dataset clearly demonstrated that varying this parameter, even to the extent of setting a negative quantity, had little effect on model output in either season. Consequently, it is unlikely that low simulated grain yields may be corrected simply by adjusting the parameters responsible for translocation since the factors associated with the water balance have already been shown to have a substantial impact on model output for this relatively dry environment.

The thermal durations of specific growth stages and the cardinal temperatures used in thermal time calculations vary greatly depending on species, variety and timescale, and are also influenced by the location of the temperature measurements (i.e. air, meristem or soil) and method of thermal time calculation (cf. Section 1.2.1 and 4.2.1). In CIRUS, potential errors involved in thermal time calculations were minimised by using meristem temperature to determine cardinal temperatures and thermal durations. However, in common with many other models and field studies, HyPAR uses air temperature instead of meristem temperature; the parameters associated with thermal time were therefore assigned compromise values according to the measurements made in CIRUS, the thermal durations reported by Lenga and Keating (1990) and Fischer

and Palmer (1984), a sensitivity analysis of cardinal temperatures and the best fit for the known durations of each growth stage in both seasons. The sensitivity analysis showed that a progressive increase in base temperature from 8 to 10 °C, spanning the range reported in the literature, increased time to maturity by 8-24 % during both simulated seasons, but affected yield only during S94/95 when AGW, Yg and harvest index were all increased (Fig. 6.9). Raising the base temperature increased simulated yields in S94/95 by restricting growth at the beginning of the season when the extended dry period caused water stress, and lengthening the season in response to the favourable late-season conditions. Altering the other cardinal temperatures had little effect on yield or growth stage duration during either season.

The duration of specific growth stages in HyPAR may be defined using either chronological or thermal time, and the relevant information for KCB4 was obtained as output from CERES-Maize. Varying the thermal durations of growth stages 1 to 3 (GS1, emergence to panicle initiation; GS2, panicle initiation to anthesis; GS3, anthesis to maturity) had the expected effect on the length of these stages when expressed in chronological time and on predicted final yields and harvest indices. The model was generally relatively insensitive to variation in the number of days assigned to the Germination, Juvenility, GrainSetTime and PartitionTime parameters under the prevailing conditions during the two modelled seasons. However, small variations in the Germination parameter (the period when seed reserves are available for mobilisation) during S94/95 had dramatic effects on simulated yields (Fig. 6.10); thus, an increase of six days from the default value of 9 increased Yg by 0.4 t ha^{-1} and AGW by 0.9 t ha^{-1}. An increase in the Germination factor effectively distributed the available assimilate over a longer period, thereby sustaining the seedlings more effectively during the dry periods at the beginning of the S94/95 season.

Hess and Stevens (1994) reported that the yields predicted by HyPAR were highly sensitive to the set values for water use ratio (W; g DW mm^{-1} water kPa^{-1}) during wet years, but were less sensitive during drier years. These workers described a sigmoidal response to increasing W for wet years in which grain yield (Yg) increased rapidly from 0.2 to 5 t ha^{-1} as W was increased between 0.0025 and 0.0065 g DW mm^{-1} water kPa^{-1}; the response was much reduced during dry years, when Yg increased linearly

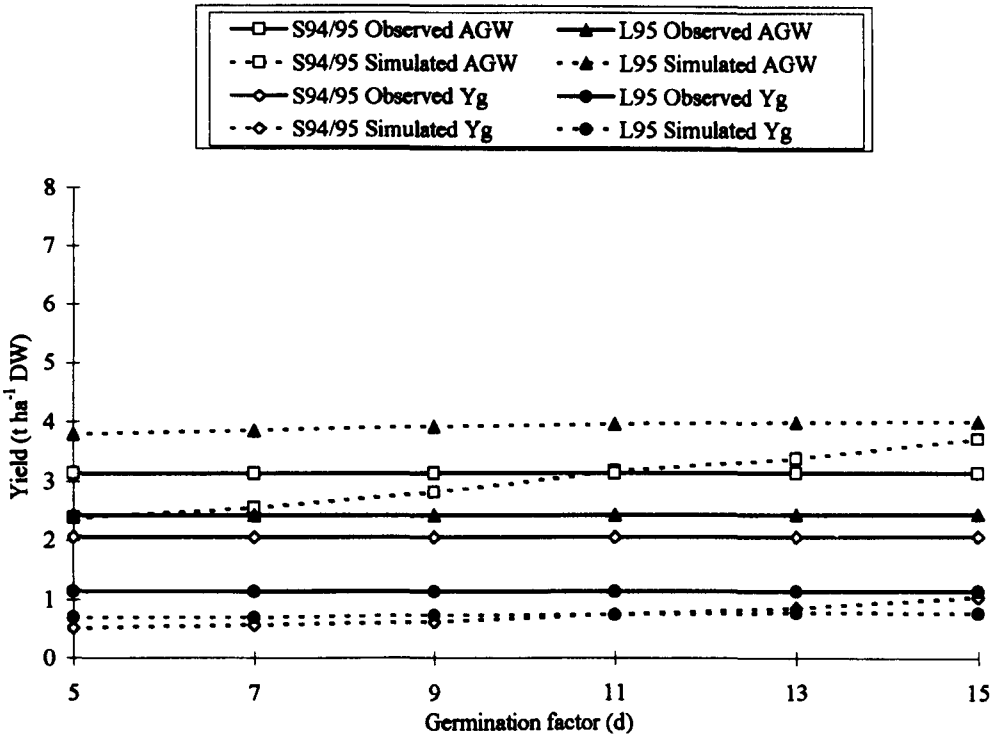

Figure 6.10 Effect of changing the Germination factor (length of time when seed reserves are available for growth) in HyPAR on simulated grain yield (Yg) and biomass (AGW) of KCB4 maize during the S94/95 and L95 seasons. Solid lines represent the observed yields in CIRUS.

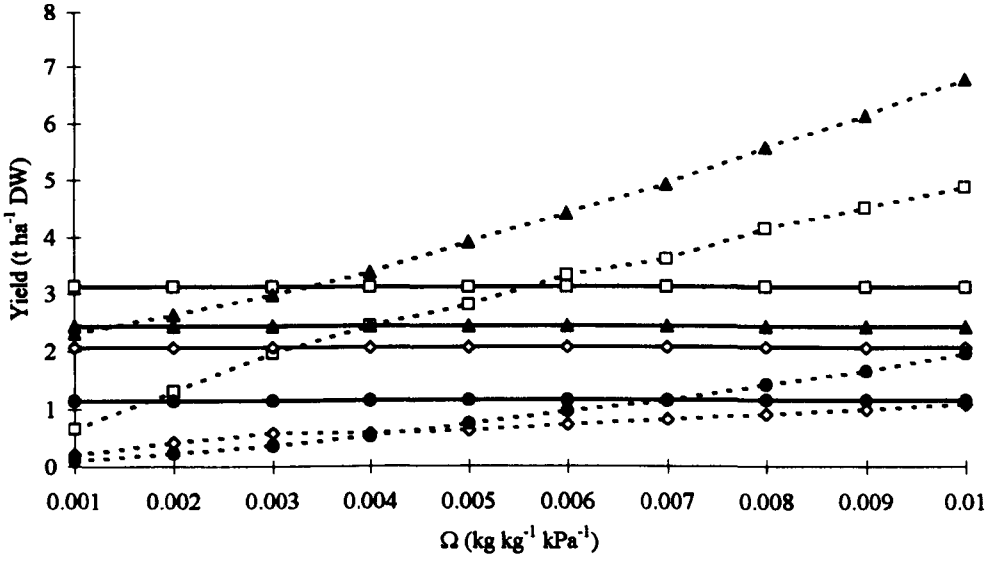

Figure 6.11 Effect of altering Ω (water use ratio) in HyPAR on simulated grain yield (Yg) and biomass (AGW) of KCB4 maize during the S94/95 and L95 seasons. Solid lines represent the observed yields in CIRUS.

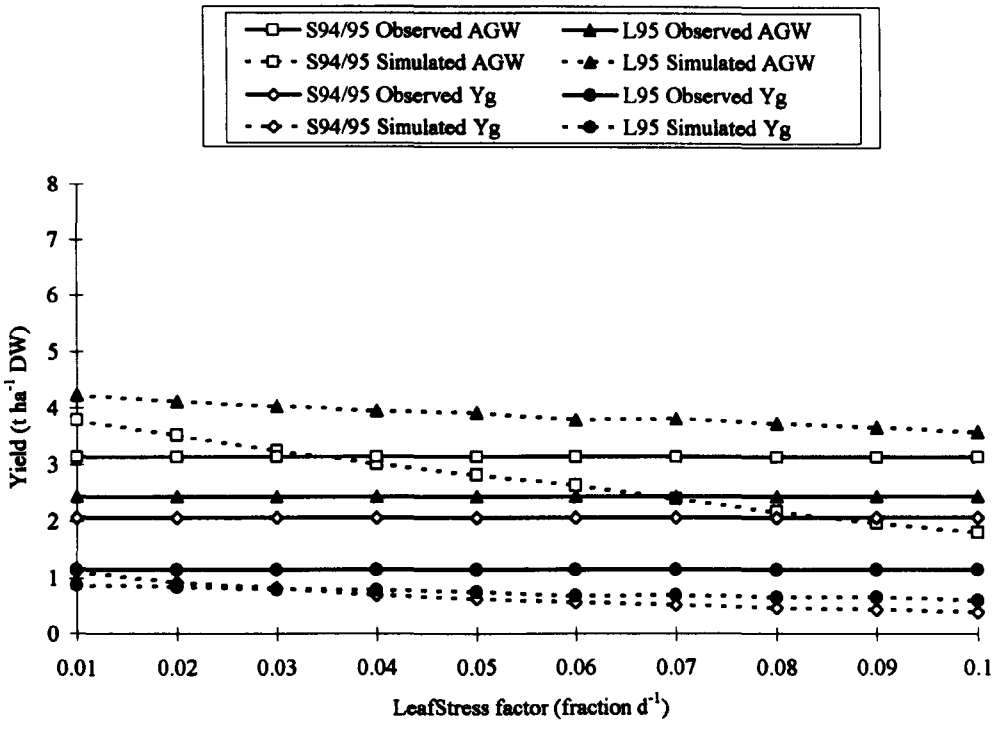

Figure 6.12 Effect of changing the Leafstress factor (proportion of leaf area dying per stress day) in HyPAR on simulated grain yield (Yg) and biomass (AGW) of KCB4 maize during the S94/95 and L95 seasons. Solid lines represent the observed yields in CIRUS.

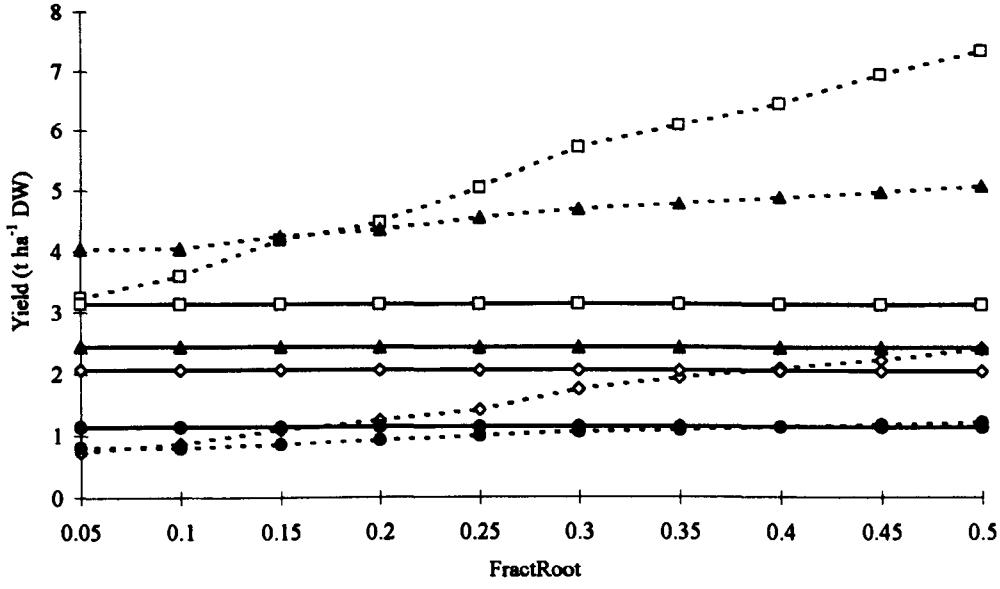

Figure 6.13 Effect of changing the FractRoot factor (proportion of total biomass present as roots when Ω, Photosynth1 and Photosynth3 were calculated) in HyPAR on simulated grain yield (Yg) and biomass (AGW) of KCB4 maize during the S94/95 and L95 seasons. Solid lines represent the observed yields in CIRUS.

from 0.1 to 0.3 t ha^{-1} over the same range of W. Hess and Stevens (1994) concluded that the inconsistency of yield responses for seasons with contrasting environmental conditions originated from the absence of reliable values for W. Sensitivity analysis of HyPAR for the S94/95 and L95 seasons over the range of W used by Hess and Stevens produced linear responses in which Yg increased from 0.30 to 1.04 t ha^{-1} during L95, and from 0.50 to 0.77 t ha^{-1} during S94/95 (Fig. 6.11). Thus, although environmental conditions were similar in the present study to those of Hess and Stevens (1994), the sensitivity of the model to W was unpredictable, with the result that W influenced yields greatly under certain conditions but had little effect under others. This observation highlights not only the absence of definitive knowledge concerning the correct value for W, but also suggests that some parameters may need to be validated independently before simulations are made under certain environmental conditions. Such independent validations would require databases which extend over wide timescales and a range of climatic conditions, and are therefore beyond the scope of the dataset presented here.

During periods of stress, the LeafStress factor reduces simulated leaf area by a fixed percentage for each day that stress persists. Hess and Stevens (1994) found that the LeafStress factor was highly influential in determining yield during dry seasons, but had little effect during wet seasons. However, sensitivity analysis of HyPAR for changes in the LeafStress factor between 0.01 and 0.1 revealed a more complex response, in which yield declined more rapidly during the wetter S94/95 season than during L95 as LeafStress increased (Fig. 6.12). This response probably resulted from a severe reduction in leaf area during the extended dry period at the beginning of the season, when most of the seasonal stress days occurred, again highlighting the complex relationship between crop growth and water availability.

HyPAR simulates the root growth of crops in two phases; Phase 1 involves the initial advance of the rooting front, while Phase 2 allocates dry matter from photosynthesis to the advancing roots. Only after Phase 2 has been completed can new roots extract water. Extensive analysis for the S94/95 and L95 seasons showed that model output was sensitive to four parameters controlling root growth, namely FractRoot (proportion of total biomass present as roots when W, Photosynth1 and Photosynth3

were calculated), RRmax (maximum daily root extension rate, mm d^{-1}), RWLfactor (carbon cost per unit root length, kg cm^{-1}) and MaxUptakeRate (maximum water uptake rate, mm mm^{-1} soil layer). Of these, FractRoot appeared to be the most important since the anomaly that higher simulated yields were obtained during the drier L95 season was reversed for both Yg and AGW when values for FractRoot of 0.2 and above were set (Fig. 6.13).

The default value for FractRoot in PARCH is zero, since the dataset for sorghum used in model development was obtained from glasshouse experiments, from which root biomass data were available for the calculation of resource use efficiency. However, this is unlikely to apply in most field studies, since reliable measurements of root biomass are both difficult and time-consuming, with the result that resource use efficiencies are often calculated on the basis of above-ground biomass alone. FractRoot must therefore be assigned a value greater than zero during parameterisation of HyPAR in most instances. Squire (1990) stated that roots comprise a large proportion of total dry weight in cereal crops, particularly in dry environments. For example, the roots comprised 34 % of total plant dry weight for pearl millet growing on stored water in Niger and 49 % for barley in Syria. Extensive coring measurements in CIRUS, reported in part by Smith *et al.* (1996), showed that the roots contributed on average c. 33 % of the total biomass in sole maize (Smith, pers. comm.), although this fraction was slightly greater early in the season (c. 39 %) and during the drier of the two seasons reported here. FractRoot was therefore ascribed a value of 0.35 for the present simulations.

Azam-Ali *et al.* (1984) reported mean root extension rates of 60-70 mm d^{-1} for millet growing under controlled environment conditions, while Pellerin and Pages (1994) recorded a mean rate of c. 80 mm d^{-1} for maize under optimal conditions. Bradley and Crout (1993) set the default for PARCH-sorghum to 45 mm d^{-1} to allow for a reduction in the maximum rate of root growth in response to sub-optimal growth conditions. Accurate measurements of root extension in CIRUS were not available, but sensitivity analysis using HyPAR revealed a curvilinear response whereby predicted yields declined rapidly at extension rates below 20 mm d^{-1} in both seasons (Fig. 6.14). Thus the value of 25 mm d^{-1} set by Hess and Stevens (1994) is probably

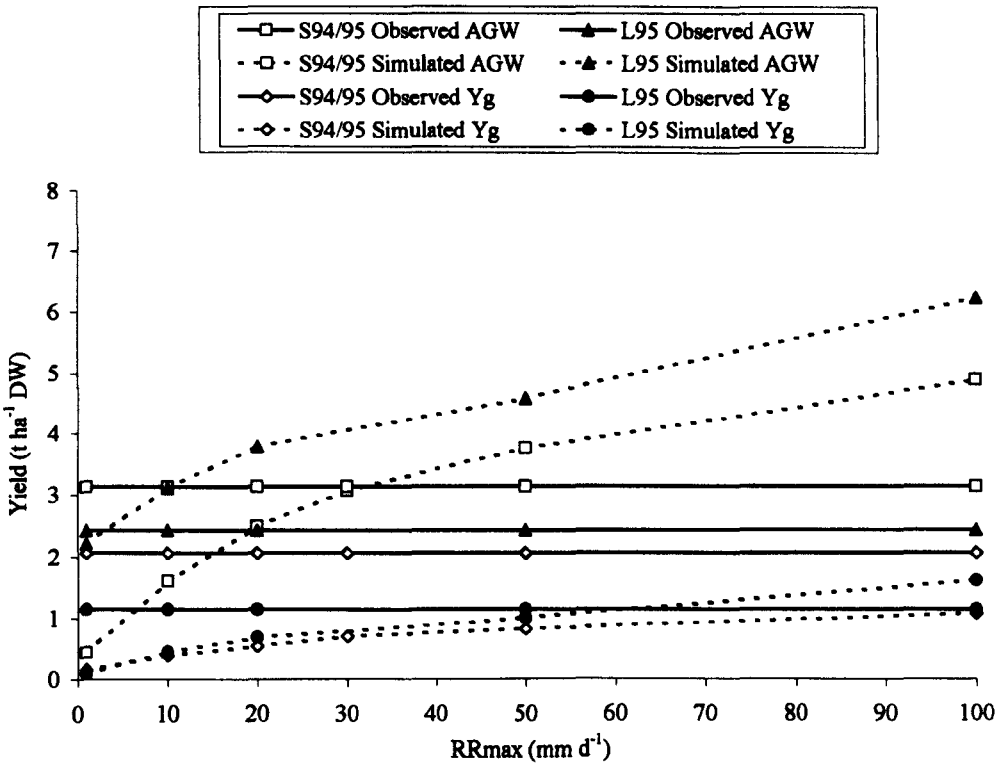

Figure 6.14 Effect of changing the RRmax factor (maximum daily root extension rate) in HyPAR on simulated grain yield (Yg) and biomass (AGW) of KCB4 maize during the S94/95 and L95 seasons. Solid lines represent the observed yields in CIRUS.

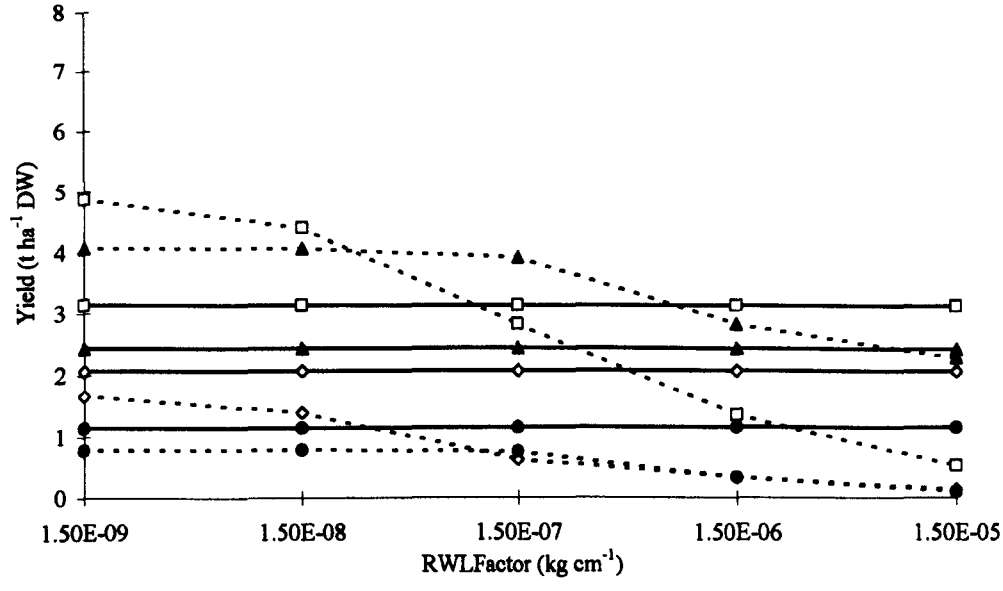

Figure 6.15 Effect of changing the RWLfactor (carbon cost per unit root length) in HyPAR on simulated grain yield (Yg) and biomass (AGW) of KCB4 maize during the S94/95 and L95 seasons. Solid lines represent the observed yields in CIRUS.

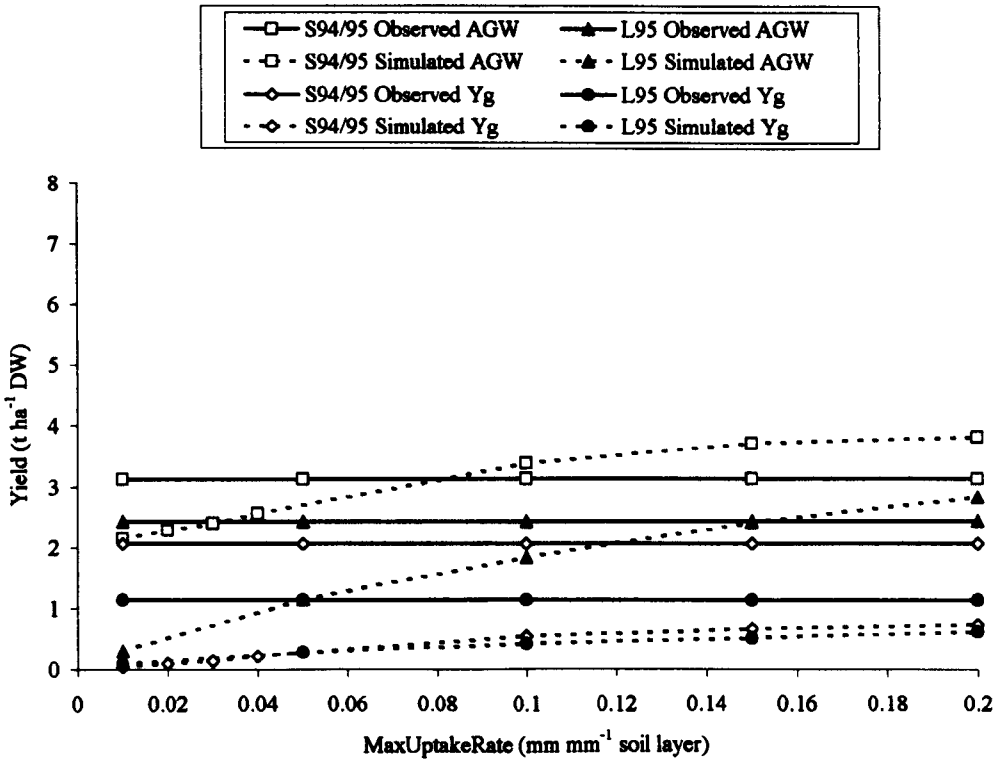

Figure 6.16 Effect of changing the MaxUptakeRate factor (maximum water uptake rate) in HyPAR on simulated grain yield (Yg) and biomass (AGW) of KCB4 maize during the S94/95 and L95 seasons. Solid lines represent the observed yields in CIRUS.

unrealistically low for maize under the prevailing conditions at Machakos and has the effect of greatly reducing predicted yields (Fig. 6.14).

Simulated yields were inversely proportional to the carbon cost of the roots (RWLFactor), although the response varied between seasons (Fig. 6.15). A c. ten-fold reduction in the default value for KCB4 from $1.5e^{-7}$ to $1.5e^{-8}$ (where e is the natural logarithmic constant, c. 2.718) altered the relationship between seasons so that predicted yields for the wetter S94/95 season were greater than in L95, in compliance with the field results. The field studies of root distribution in CIRUS (Smith *et al.*, 1996) could not supply the information required to parameterise the RWLFactor specifically for Katumani composite maize in CIRUS and it was difficult to find suitable information within the literature. Indeed the default value recorded for KCB4 was taken unchanged from the general sorghum default value in PARCH. Therefore, since a three fold reduction in root carbon content is well within the variation observed for roots of varying diameter on the same plant (Thomas *et al.*, 1996), such a reduction should be acceptable when defining root carbon density using a default value based on another species.

Although the default value for the MaxUptakeRate factor in sorghum is set at 0.1 mm mm^{-1} (Robertson *et al.*, 1993), Hess and Stevens (1994) increased the value for KCB maize to 0.2 mm mm^{-1} soil layer, equivalent to the maximum allowable in HyPAR. Sensitivity analysis across the input range (0.01-0.2 mm mm^{-1}) for the current dataset demonstrated a curvilinear response of modelled yields as MaxUptakeRate increased (Fig. 6.16). It therefore appears likely that the maximum value of 0.2 mm mm^{-1} assigned by Hess and Stevens would substantially increase simulated yields. The maximum water uptake rate (MaxUptakeRate) for maize in CIRUS was estimated to be 0.3 g h^{-1} m^{-1} root length (Smith, pers. comm.) from measurements of the hydraulic conductance of whole root systems. This corresponds to an extraction rate of c. 0.01 mm water mm^{-1} soil layer d^{-1}, equivalent to the minimum input value allowed by HyPAR, which would greatly reduce simulated yields relative to those produced by the extraction rate assigned to KCB4 in the model (0.2 mm water mm^{-1} soil layer d^{-1}; Fig. 6.16).

Table 6.9 Cultivar file (*KCB97*) for Katumani composite B maize. Blocked areas indicate values modified from *KCB4* (Table 6.1) after extensive sensitivity analysis on selected parameters.

Definition of parameter	Parameter code	Value	Units
Minimum partition of photosynthate to leaves during GS1 and GS2	minFL	0.1	proportion
Maximum partition of photosynthate to leaves during GS3	maxFL	0.8	proportion
Maximum partition of photosynthate to haulm during GS3	maxFH	0.1	proportion
Reserved for future expansion	null	0	-
Reserved for future expansion	null	0	-
Reserved for future expansion	null	0	-
Fraction of carbon to roots before stress adjustment	oFBG	0.25	proportion
Fraction of stem available for translocation	TransPot	0.3	proportion
Maximum fraction of stem available for translocation that can move per day	DayTransPot	0.1	fraction d^{-1}
Time for seed to use carbon supplies	**germination**	**15**	% C d^{-1}
Duration of plant juvenility - thin roots and leaves	Juvenile	11	d
Time from anthesis to grain set	**GrainSetTime**	**5**	d
Minimum time for grain filling	**PartitionTime**	**37**	d
Base cardinal temperature for growth	**tb**	**10**	°C
Maximum cardinal temperature for growth	**tm**	**45**	°C
Point where an increase in temperature has no more effect on growth	tbplateau	28	°C
Start of thermal denaturation - induces stress	**tmplateau**	**32**	°C
Reduction in thermal time accumulation as a result of stress prior to anthesis	GS1ttFactor	0.1	dimensionless
Increased maturity rate as a consequence of stress after anthesis	GS3ttFactor	0.03	dimensionless
Thermal time for Growth stage 1	GS1tt	223	°Cd
Thermal time for Growth stage 2	**GS2tt**	**352**	°Cd
Thermal time for Growth stage 3	**GS3tt**	**634**	°Cd
Tolerance of crop to water stress	STindex	3	dimensionless
Rate of recovery from stress	Recovery	0.5	% d^{-1}
Reduction in translocation rate as a consequence of stress	**STransReduct**	**0.5**	dimensionless
Impact of stress on specific leaf area	SLAstress	0.7	dimensionless
Fraction of leaf area senescing per day as a consequence of stress	**LeafStress**	**0.03**	fraction d^{-1}
Increase in the fraction of carbon allocated to roots as a consequence of stress	RstressFBG	0.3	proportion
Maximum reduction of root extension rate as a consequence of stress	maxRstress	0.8	proportion
Maximum proportional reduction in light interception due to leaf rolling	lrollmax	0.4	proportion
Specific leaf area during Growth stage 1	SLA1	35	m^2 kg^{-1}
Specific leaf area during Growth stage 2	SLA2	25	m^2 kg^{-1}
Maximum leaf area for plants in a sparse canopy	MaxPlantArea	0.5	m^2
Rate of phenological death	LIFEC	0.5	dimensionless
Radiation conversion efficiency for Growth stage 1	**Photosynth1**	**1.7**	g MJ^{-1}
Radiation conversion efficiency for Growth stage 3	**Photosynth3**	**1.1**	g MJ^{-1}
Light extinction coefficient	k	0.65	dimensionless
Transpiration equivalent	qD	0.005	kg C kg^{-1} water kPa^{-1}
Conversion factor for grain number	**GNC**	**10**	dimensionless
Maximum grain weight	**MaxGW**	**0.41**	g
Minimum rooting depth	RDmin	20	mm
Maximum daily root extension rate	**RRmax**	**40**	mm d^{-1}
Maximum root length per unit volume	RLVmax	5	cm cm^{-3}
Roots are x-times thinner at germination	emRWLfactor	6	dimensionless
Roots are x-times more likely to grow downwards at germination	emRDfactor	4	dimensionless
Quantity of carbon per unit root length	**RWLfactor**	**$1.5e^{-8}$**	kg C cm^{-1}
Vertical roots are x-times thinner than average roots	FineRoot	12	dimensionless
Maximum water uptake rate	**MaxUptakeRate**	**0.01**	mm mm^{-1}
Root distribution half-depth function	Rdist	300	mm
Maximum rooting depth	**maxRdepth**	**1100**	mm
Permanent wilting point of plant	pWiltp	45	m
Fraction of soil saturation when plants experience waterlogging	WLsat	0.95	proportion
Factor to reduce the water uptake rate in response to waterlogging damage	**WLdamage**	**0**	dimensionless
Daily waterlogging recovery rate	**WLrecover**	**1**	fraction d^{-1}
Sensitivity to waterlogging of a portion of the root system	**WLsuscept**	**1**	proportion
Rate of population decline in response to waterlogging	**WLdeath**	**0**	fraction d^{-1}
Proportion of plant that was root when 'Ω' and 'Photosynth' were calculated	**FractRoot**	**0.35**	proportion

Table 6.10 Yields and growth stage durations observed in CIRUS compared with output from HyPAR after the second validaion for a) S94/95 and b) L95. Data are shown for maize grown as a sole crop (Cg) or in the dispersed agroforestry treatment (CTd). Observed and first validation results are repeated from Table 6.8 to facilitate comparison.

a) S94/95	Observed		Second Validation		First Validation	
	Cg	CTd	Cg	CTd	Cg	CTd
Grain yield (t ha^{-1})	2.06	0.82	2.19	1.51	0.62	0.04
Total dry matter (t ha^{-1})	3.13	1.48	3.18	2.22	2.82	0.21
Duration of growth stage 1 (d)	20	21	21	21	18	18
Duration of growth stage 2 (d)	33	35	35	36	33	48
Duration of growth stage 3 (d)	70	66	63	62	80	39
Duration of growing season (d)	123	122	119	119	131	105
Seasonal rainfall (mm)	635	635	635	635	635	635

b) L95	Observed		Second Validation		First Validation	
	Cg	CTd	Cg	CTd	Cg	CTd
Grain yield (t ha^{-1})	1.14	0.14	3.04	1.00	0.74	0.01
Total dry matter (t ha^{-1})	2.43	0.31	6.01	3.41	3.92	2.07
Duration of growth stage 1 (d)	20	30	20	20	17	17
Duration of growth stage 2 (d)	29	40	32	32	44	47
Duration of growth stage 3 (d)	63	32	69	68	40	41
Duration of growing season (d)	112	102	121	120	101	105
Seasonal rainfall (mm)	311	311	311	311	311	311

6.5 SECOND VALIDATION

A revised crop parameter file, KCB97 (Table 6.9), was developed to replace KCB4 on the basis of the preceding sensitivity analyses. In addition, due to the high proportion of rainfall that is simulated as runoff, infiltration rate in the soil parameter file was increased from 0.6 to 1.0 and the three thin (5 mm deep) soil surface layers were reduced to one to allow the PARCH hydrology sub-model to simulate greater infiltration. Table 6.10 illustrates the predicted yields, harvest indices and growth stage durations produced by HyPAR using the revised crop parameter file and compares them with both the observed field data and output from the first validation. Simulated yields for the wet S94/95 season were slightly greater than the observed values for the sole crop (by c. 6 and 2 % respectively for Yg and AGW), which represents a considerable improvement on the simulated yields obtained during the first validation. Similarly, the simulated yields for CTd maize were much improved during the second validation compared to the first, although there was still a considerable discrepancy between the observed and simulated values for AGW and Yg; these were respectively c. 50 and 84 % greater than the observed values. Simulated harvest indices for the CTd and sole maize were comparable (0.68 and 0.69 respectively), suggesting that the presence of trees within the simulation affected Yg and AGW equally. However, the observed harvest index for the CTd maize was much lower than that for sole maize (0.55 *vs.* 0.66 respectively), suggesting that HyPAR failed to model accurately the substantial suppression of grain yield which occurred in CTd maize during this season, which probably originated from late-season soil water deficits caused by competition for water with the trees. Simulated yields greatly exceeded the observed values for both the sole and CTd maize in L95, by up to ten-fold difference in one instance. In addition, the extremely high simulated yields for L95 indicate that the anomalously higher yields observed previously for the drier of the two simulated seasons was repeated, despite the adjustments made to the FracRoot and RWLfactor parameters following the earlier sensitivity analyses. The simulated growth stage durations for L95 were also 9 and 18 days longer than those observed, suggesting that the model was unable to take account of the impact of late-season drought, particularly on the agroforestry crop. Clearly the model in its current

form cannot adequately account for crop responses to inter-seasonal variation in environmental conditions, particularly with respect to the hydrological components.

6.6 CONCLUSIONS AND RECOMMENDATIONS

The present study concentrated primarily on model output for crop growth and largely ignored tree growth for two reasons; firstly, it was felt that modelling crop growth for two seasons with contrasting environmental conditions would make the most appropriate use of the experimental dataset within the time available. Secondly, the total simulation period for the two cropping seasons of 10 months was unsuitable for assessing the performance of the tree growth sub-routines within HyPAR for the reasons outlined below. As model predictions for the sole crops were poor for both seasons during initial model validation, extensive sensitivity analyses were carried out with the objective of identifying deficiencies within the input parameters and sub-routines and improving model output. The principal conclusions are summarised below.

6.6.1 Inconsistency of parameter sensitivity

As suggested by Ong at the DFID Agroforestry Modelling Workshop at Newbattle Abbey in May 1997, every field season produces differing interactions as the climatic and soil conditions change and the influence of individual agroforestry components alters as the trees grow larger and their competitive influence increases. Effective simulation models must be sufficiently robust to cope with these changing conditions and interactions, whilst requiring only generalised parameterisation. However, the anomaly that predicted yields were higher during the drier season and the inconsistency of model sensitivity to some parameters in the two simulated seasons demonstrated that some input parameters (e.g. initial soil water content, radiation and water use efficiencies) may require independent validation under certain environmental conditions. Such a requirement could undermine a major purpose of generic models, which is to predict system yields in new environments or over extended periods in areas where extensive interseasonal variation may occur.

6.6.2 Tree/crop interactions during the annual cycle

HyPAR simulates resource capture by trees and crops at daily intervals, but permits only the crop to 'grow' on a daily timestep. Consequently, since the trees 'grow' only on an annual timestep, the model cannot accurately reproduce the constantly changing understorey microclimatic conditions during the annual cycle, to which crop growth and development respond. For example, the total biomass and leaf area of the tree canopy in the dispersed agroforestry (CTd) treatment in CIRUS increased by 3 t ha^{-1} and 13 m^2 $tree^{-1}$ respectively during S94/95 (Fig. 3.3), greatly increasing the severity of above and below-ground competition between the trees and crops. In addition, the trees in agroforestry systems are often heavily managed by periodic pruning to minimise their competitive impact on understorey crops, thereby altering the nature of the interactions between the tree and crop components. By simulating tree growth on a daily timestep and incorporating a tree management sub-routine into its structure, the model would be able to simulate more accurately the effects of the changing understorey environment.

6.6.3 Allometric estimation of canopy size

Inclusion of tree management within HyPAR would require revision of the existing sub-routine for calculating leaf area and foliar carbon content from sapwood area which is determined from measurements of trunk diameter at breast height. This approach cannot account for reductions in canopy size resulting from pruning. It is also known that allometric relationships may be compromised in agroforestry trees because pruning not only reduces leaf area but may also induce premature transformation of sapwood to heartwood as a result of the decreased transpirational demand for water (Nygren *et al.*, 1993). Reliable allometric procedures which are appropriate to the pruning system adopted, such as that described by Lott *et al.* (1998) based on measurements of trunk diameter immediately below the canopy when whole branches were successively pruned from the base of the canopy, are therefore essential for determining the canopy characteristics of agroforestry systems.

6.6.4 Accumulation of thermal time

The thermal environment experienced by crops in agroforestry systems differs from that of sole crops (Fig. 4.1) and this, coupled with treatment differences in soil water availability, may result in differing rates of thermal time accumulation (Fig. 4.8), particularly during seasons of low rainfall. The timing of growth stages therefore varies between sole and agroforestry crops. It is important that HyPAR, as well as other process-based simulation models, should be capable of simulating such differences in the duration of cropping cycles if they are to aid management decisions, particularly in areas where consecutive cropping seasons follow closely and the maturation of agroforestry crops may be delayed sufficiently that the harvest has not been completed when the ensuing growing season begins. In practice, this results in the wetting and possible lodging of the first crop, making harvest and storage difficult, and delays the planting of the succeeding crop, thereby increasing the risk of crop failure. From a modelling viewpoint, the delayed maturity of the first crop may create difficulties in terms of setting an appropriate planting date for the next.

6.6.5 Model output

Output from the version of HyPAR available for this study (July, 1997) was largely confined to crop and tree yields, crop growth stage durations and annual rainfall. It is therefore frustrating that, despite comprehensive simulation of resource capture and use by the tree and crop components, considerable detail was unobtainable as a down-loadable option or automatically plotted, as in the PARCH model. Such detail may not be required by all end-users, but would be a useful tool to aid in system design, particularly with a view to assessing the impact of the timing of tree management on crop growth and productivity.

6.6.6 Parameterisation of HyPAR

HyPAR is a highly complex model containing numerous parameters which must be defined. Although the experimental database obtained in CIRUS provided the required information for most input files, many end-users would have to rely on information from the literature, often for different genotypes or sites, to derive values for most of the parameters required, conceivably limiting the reliability of their simulations. This may be illustrated by comparing the simulated crop yields obtained during the first and second validations, since the former relied more heavily on published information to parameterise the model. The CIRUS programme also provided detailed information on soil hydrological properties, which proved to be extremely influential in determining simulated crop yields, particularly the starting soil water content and moisture content at depth. Detailed information of this type would not be available to most end-users despite its apparent importance for the effective functioning of HyPAR. It would also be extremely helpful if detailed explanations of each parameter and its relative importance in influencing model sensitivity were provided to aid parameterisation, ideally in the form of a drop-down menu accompanying the model.

6.6.7 Flexibility in defining the meteorological input file

Although the meteorological input file was designed with the minimum dataset in mind, this is likely to be the most detailed of the datasets available to end-users as model input but may well have been collected in a different form from that required by HyPAR. For example, daily saturation deficit is calculated relatively crudely in HyPAR from measurements of relative humidity at 0700 and 1400 h local time; thus, even if saturation deficit is recorded over shorter time intervals, as in CIRUS, this information cannot be used. HyPAR should therefore incorporate greater flexibility in defining the climate input file to allow users to customise it to match the available data.

6.6.8 Complications with extended simulations

Modelling agroforestry systems from planting to maturity requires simulations extending over periods of years, but several factors within the model currently make this difficult. Firstly, tree death during establishment is common in HyPAR simulations, but is much less likely under field conditions because the trees in most agroforestry systems are intensively managed. Secondly, HyPAR limits the number of cropping seasons during each annual cycle to one, even though the bimodal rainfall in many tropical areas allows two cropping seasons per year. Thirdly, only one crop species can be modelled during each simulation cycle, whereas in reality spatial or temporal intercropping is often practised, involving concurrent or sequential mixtures of crops within the same annual cycle. Substitution of alternative crops during the lifespan of individual agroforestry systems also offers a viable approach to maintaining system productivity despite the increasing demand for resources as the trees grow larger. Successful process-based models should be capable of simulating such spatial and temporal variation in the crop species grown in agroforestry systems. Finally, HyPAR preferentially allocates resources to the tree component, creating an inherent tendency to underestimate the competitive impact of associated crops on tree growth during the establishment period.

6.6.9 Rounding errors

The estimates of tree height provided by HyPAR are rounded to the nearest metre, representing a potentially serious loss of resolution even in fast-growing species such as *Grevillea robusta*, in which height increases by c. 2 m per year. Thus a simulated height increment of 1.5 m would be rounded to 2 m, potentially introducing an error of 33 %.

6.6.10 Poor simulation of infiltration

There is clearly a need to improve the hydrology model to simulate water movement through the soil profile, as has previously been recognised (Lawson *et al.*, 1996). The present study has highlighted serious difficulties concerning the infiltration of water to

depth in the soil profile which have major implications for the success of crop growth simulations, particularly when the initial soil water content is low; the development of revised hydrological sub-routines within HyPAR may rectify this problem.

CHAPTER 7

FINAL DISCUSSION AND CONCLUSIONS

7.1 SUMMARY OF RESULTS

This project sought to determine the consequences of establishing overstorey agroforestry systems in a semi-arid environment on the productivity and resource capture of both trees and crops. Land equivalent ratios for the dispersed agroforestry (CTd) system were greater than or equal to unity for all nine cropping seasons (Fig. 3.13). However, this apparent advantage of agroforestry during some seasons as the system matured, masks the complexity of the interactions between system components and the prevailing environmental conditions. Consideration of the performance ratios of the tree and crop (Fig. 3.12) showed that the growth of CTd grevillea was initially very low, but that the values approached unity after c. 32 months; those for the crop exhibited the converse trend by remaining close to unity for the first three growing seasons, but declined to near zero during three of the final four seasons. These trends suggest that, irrespective of crop type and tree size, competitive interactions between the two components for the same resource pool invariably occurred.

Significant differences in size between the sole (Td) and agroforestry (CTd) trees were established during the first 130 days after planting (Figs. 3.1 and 3.2). The slower initial growth of the CTd grevillea was probably attributable to the greater frequency and severity of drought, resulting from competition for water with associated crops during the tree establishment phase and the possibly detrimental effect of shading by the maize canopy during the second cropping season (L92). However, competition with associated crops was not confined to the establishment period. For example, neither canopy biomass nor LAI differed significantly between the Td and CTd trees during the early part of the unusually wet 1994/95 short growing season (S94/95), but by the end of this season the canopy of the CTd trees was significantly smaller, suggesting that below-ground resources had been depleted more rapidly as a result of competitive extraction by the associated maize. As a consequence of competition with the associated crops, the standing biomass and trunk length and taper characteristics of the CTd trees were

inferior to those of Td trees throughout the experimental period and this effect could be expected to persist until tree harvest at approximately 8 years after planting. Since the principal economic return from grevillea is as construction poles, the inferior length and taper characteristics of the CTd trees would seriously undermine the economic potential of this agroforestry system. Indeed, Peden *et al.* (1996) reached a similar conclusion following a survey of 15 tree species, including grevillea, grown in various agroforestry systems for pole production.

Of the nine cropping seasons in CIRUS, seasons 1, 3 and 5 (S91/92, S92/93 and S93/94) were planted with cowpea and the remainder with maize. During the first three seasons, crop yields in the CTd treatment were similar to those for the corresponding sole crops (Cg 0%; Fig. 3.10), even though rainfall varied greatly (404, 261 and 773 mm respectively) and different crops were grown (cowpea, maize, cowpea). During the fourth cropping season, the rains failed (112 mm), causing complete crop failure. However, the grevillea continued to grow rapidly in the absence of competition from associated crops, by exploiting reserves of water deep in the soil profile and residual water remaining from the preceding unusually wet season which was unavailable for crop establishment. Consequently, by the following season (S93/94; cowpea), CTd grevillea had attained a LAI of 0.5 and a height of c. 3 m. As a result, competition with the understorey crops during the remaining five seasons shifted in favour of the now well established tree component, initially with a c. 40 % decline in cowpea yields during S93/94 relative to the sole crop. During the final four seasons (L94-S95/96), above-ground biomass was greatly reduced in CTd maize relative to the Cg 0% sole crop, with almost no yield being obtained in three of the four seasons (Fig. 3.6). Only during S94/95, when the rainfall was well above average (628 mm *vs.* long-term average of 414 mm) was yield within 50 % of that for sole maize (Fig. 3.6b). Estimates of standing biomass and LAI showed that the impact of competition was apparent from the early stages of the final two growing seasons, but that the intensity of competition decreased with distance from the tree.

The shade net experiments carried out during the final four cropping seasons simulated the shading effect of the tree canopy in the absence of competition for water and nutrients. Above-ground biomass and grain yield of maize grown in the shade net

treatments were invariably greater than CTd maize and approximately equal to the unshaded Cg 0% treatment under 25 % shade, except for the S94/95 season when grain yield in the Cg 25% treatment was c. 60 % of that in the Cg 0% treatment despite an abundant supply of soil moisture. This suggests that shading was detrimental to maize growth only when soil moisture was non-limiting. Measurements of net photosynthetic rate (Pn) showed that the Pn of the Cg 25% maize was significantly lower early on in the S94/95 season (c. 30 DAS) than in the Cg 0% treatment (Fig. 4.9), with the result that assimilate production would have been reduced. This culminated in the standing above-ground biomass being significantly lower in Cg 25% maize than in the Cg 0% treatment at the time of anthesis (Fig. 3.7). During seasons of near or below average rainfall, artificial shade did not decrease the productivity of maize, probably because Pn was already limited by partial stomatal closure in the sole stand (McPhearson and Slatyer, 1973). This hypothesis is supported by the light response curves established during S95/96 since those for Cg 25% and Cg 0% maize were never significantly different and approached light saturation over the upper 40 % of the PAR flux range examined. Consequently, a 25 % reduction in PAR from a generally high incident level (1600-1800 mmol m^{-2} s^{-1}) would have been expected to have little effect on Pn in Cg 25% maize relative to Cg 0% maize; since the mean seasonal reduction in incident radiation resulting from tree shade was c. 30 %, the Pn values for understorey maize would also not have been expected to be reduced in the absence of below-ground interactions. There was also no significant difference between the diurnal timecourses of Pn and stomatal conductance (g) at the time of anthesis during S95/96 (Fig. 4.11), although there was some indication that higher g and Pn values were maintained later in the day in Cg 25% maize, suggesting that these plants experienced less severe water stress than the Cg 0% maize. These observations indicate that the shade provided by overstorey trees may not be responsible for the yield reductions obtained for understorey maize during seasons of low rainfall, when competition for water between the tree and crop would have exacerbated the severity of the water stress experienced by the latter. However, even when soil moisture stress is alleviated during seasons of heavy rainfall, shading by the tree canopy may be expected to induce significant yield reductions. Thus, the grevillea/maize agroforestry system examined in the present study exhibited little potential for spatial complementarity.

The presence of the tree canopy in the dispersed agroforestry (CTd) treatment reduced the mean daily quantity of radiation received by the understorey crops. The degree of shading increased as the tree canopy expanded, although the pruning regime limited the maximum shading intensity to c. 30 %. However, this reduction in incident radiation was not uniform because the discontinuous nature of the tree canopy caused substantial local variation in shading intensity depending on proximity to the trees and solar angle (Fig. 4.5). Seasonal mean fractional interception was greater for the combined canopies of the CTd treatment during S94/95 than for either of the sole canopies, suggesting that the productivity of the agroforestry system was potentially greater. As rainfall during S94/95 was well above average (628 mm *vs.* 350 mm), this apparent spatial complementarity was probably the result of the increased soil water availability. Howard (1997) also reported that seasonal mean fractional interception was greatest in the CTd treatment during the previous two short growing seasons (S92/93 and S93/94), when soil moisture status was also relatively high and competition for soil moisture was therefore reduced. Under the less favourable soil moisture regimes which prevailed after S94/95, fractional interception would be expected to be less in CTd than in the Td treatment due to the smaller tree canopy and severely limited growth of the understorey crops (Fig. 3.7).

Shading by the tree canopy and artificial shade nets substantially modified the understorey thermal environment (Fig. 4.1). However, the extent of the observed temperature moderation was less during the final two experimental seasons for the CTd treatment because the continued growth of the trees and pruning of the basal branches allowed greater air movement within the understorey environment. The extent of temperature modification during the establishment of this dispersed overstorey agroforestry system may therefore be approximated by a bell-shaped curve to describe the exponential increase in temperature moderation which occurred as the canopy expanded and the subsequent decline resulting from tree growth and basal pruning. A fuller understanding of such curves and their effects on understorey crop growth might allow the temperature environment to be manipulated to maximise the positive influence of microclimatic changes. Temperature moderation may be advantageous in semi-arid environments where sole crops experience temperatures exceeding their optimal range for a significant proportion of their growth cycle, such as, the high mid-day soil

temperatures (45-55 °C) prevalent in agricultural land in Rajasthan (Khalifa and Ong, 1990). However, if the thermal environment becomes less favourable, the rate of development is likely to be slowed. For example, the 15 day delay in flowering observed in CTd maize during the L94 season could be attributed solely to the slower accumulation of thermal time relative to Cg 0% maize. The consequences of such a substantial delay might be highly detrimental for crop productivity in semi-arid environments for two reasons. Firstly, although the bimodal rainfall permits two cropping seasons per year, the period between the harvest of the first crop and the onset of the second cropping season is normally extremely short. Any significant delay in development might therefore result in the first crop not reaching full maturity or drying insufficiently before the onset of the second rainy season, resulting in potentially catastrophic yield losses. In addition, if the subsequent crop is planted late, due to delays in the cultivation of the land, its yield may also be compromised. Secondly, any delay in development would impair the ability of the crop to compete with trees for available resources by slowing the establishment of both the roots and the canopy. Slow crop establishment could also result in a higher total loss of moisture through evaporation due to poor ground cover and low crop water uptake, which could further increase the risk of water stress. The establishment of overstorey agroforestry systems should therefore be confined to areas of the semi-arid tropics where high temperatures are prevalent and temperature moderation is advantageous for crop growth; in such systems, the tree canopy should be managed to maximise these beneficial effects. In areas where the sole crop does not normally experience excessively high temperatures, the tree canopy should be managed to minimise the negative effects of temperature moderation by maintaining the base of the canopy as far above the crop as possible to increase air movement.

Previous studies have suggested that grevillea has a high potential for complementarity because it has few lateral roots and may extract up to 80 % of its water from below the crop rooting zone (Mwihomeke, 1992; Howard, 1997; Howard *et al.*, 1997). However, consideration of both tree and crop growth in the CTd treatment clearly demonstrates the existence of below-ground competition between these components, suggesting the occurrence of substantial activity by tree roots within the crop rooting zone. This was confirmed using heat balance gauges adapted for use on grevillea roots (Lott *et al.*, 1996), which showed that the lateral roots of grevillea extracted substantial quantities of

water from the crop rooting zone at distances of up to 2 m from the trunk during periods when the surface soil horizons were relatively wet. Further studies during dry periods demonstrated that there was considerable variation in the distribution of water uptake by trees of similar size. These results suggest that, although considerable quantities of water may be extracted from below the crop rooting zone, the potential for deep extraction depends greatly on soil depth, the presence of fissures in the underlying bedrock and the ability of roots to extract the available water. Thus, if the soil moisture potential is higher in the surface soil layers than at depth, extraction from these horizons would be favoured (Adar *et al.*, 1995; Smith, 1995). The availability of water in the surface layers and site-specific factors may therefore modify both root distribution and function and must be distinguished from genetically determined traits in order to identify which pedological and environmental conditions enable grevillea and other tree species to exhibit complementarity.

Rainfall outside the cropping season contributed c. 10 % of the total annual precipitation. Since the trees continued to grow during the off-season periods, they were able to utilise this rainfall which might otherwise have been lost from productive use (Ong *et al.*, 1992). However, the continued growth of grevillea would also have depleted residual water supplies, which might otherwise have been utilised by the crop during the following growing season. For example, mean dry season water use by grevillea during the D95 season was 0.6 mm d^{-1}, equivalent to a cumulative water use between the L95 and S95/96 cropping seasons of c. 60 mm, while rainfall during this period was only 19 mm. Consequently, since sap flow measurements demonstrated that trees preferentially extracted water through lateral roots when the soil moisture in the surface horizons was relatively high, tree water uptake could significantly reduce the moisture content of the crop rooting zone during the dry season. This would be to the detriment of crop productivity during subsequent growing seasons. The apparent advantage of the tree component of agroforestry systems in utilising off-season rainfall in semi-arid environments may therefore highlight poor complementarity within the system, by demonstrating the capacity of trees to extract water from within the crop rooting zone.

7.2 AGROFORESTRY SYSTEM DESIGN FOR SEMI-ARID ENVIRONMENTS

Trees and shrubs are essential elements in the overall stability of the rural economy and inseparable components of rural land use management (Ben Salem, 1980; Ben Salem and Palmberg, 1985). They should therefore not be relegated to a secondary role, but form an integral component of developing agricultural systems. Selection, breeding and management programmes for the development of improved agroforestry systems should therefore focus on both the tree and crop components to ensure their suitability for use within an agroforestry context and to maximise system productivity. The importance of computer simulation modelling in identifying appropriate characteristics for breeding and selection and assessing management practice cannot be understated.

7.2.1 Choice of tree species for agroforestry

The potential for spatial complementarity under semi-arid conditions depends heavily on the complementary utilisation of below-ground resources by the components of agroforestry systems. When the tree canopy has become established, modification of thermal conditions may be beneficial for understorey crops, while reductions in incident radiation may not be detrimental for crop growth in some semi-arid environments; however, neither of these potentially positive above-ground attributes of agroforestry will be realised if below-ground competition is severe. Considerable effort has therefore been expended to classify the rooting patterns of trees in an attempt to identify species or provenances with predominantly deep rooting habits which are potentially useful for agroforestry. However, as root distribution alone is not necessarily an accurate indicator of the inherent patterns of water extraction, as shown in the present study, studies of the distribution of water uptake throughout the year using sap flow techniques or isotopic discrimination (Flanagan *et al.*, 1992; Smith, 1995) will be invaluable in identifying tree species which exhibit appropriate below-ground complementarity. Information for each tree species should be collected across a range of site conditions, including both deep and shallow soil, to establish the effects of site-specific factors which modify genetically-determined root distribution and water extraction characteristics.

Complete spatial complementarity in semi-arid environments is extremely unlikely since, although trees may be capable of exploiting deep water reserves beneath the crop

rooting zone, they will preferentially extract surface supplies when these are abundant following rainfall (Smith, 1995). Temporal complementarity is therefore likely to provide a better alternative to spatial complementarity, since competition for water is minimised by the tree and crop canopies being maintained out of synchrony as a consequence of their differing phenology or a planned pruning regime. For example, the much-cited *Faidherbia albida* loses its leaves prior to the rainy season and therefore does not compete initially for water with understorey crops; these in turn benefit from the partial shade, higher soil organic matter and enhanced soil fertility provided by the trees (Monteith *et al.*, 1991).

Selection of *Grevillea robusta* provenances for agroforestry has focussed on height and growth rate (Kallinganire and Hall, 1993), while ICRAF's selection programme for trees suitable in general for agroforestry has concentrated on stem height, diameter, straightness, bole form, wood density and crown diameter (Esegu and Odoul, 1992). However, Howard (1997) suggested that characteristics which improve complementarity represent more appropriate selection criteria, while Harwood and Owino (1992) proposed that a sparse and narrow crown and deep rooting habit were desirable traits. Although attributes which improve complementarity are desirable, it is essential that the search for such characteristics does not compromise the economic potential of the system. Complementarity may be enhanced by adopting appropriate management practices, such as reducing the planting density of the trees, provided the economic value is sufficiently high to compensate for the decreased population. A tree with limited economic value is of little benefit to resource-poor farmers irrespective of the extent of its complementarity with understorey crops. In France, for example, high value tree species such as walnut have been bred specifically for use in agroforestry systems because agroforestry grown walnut provides better economic return than trees grown in plantations and natural forests. This is because the site preparation, fertility enhancement and cultivation methods practised by farmers in agricultural fields, result in more uniform and better quality tree growth (Owino, 1996). As the sites used for plantation forestry tend to be only slightly modified relative to agricultural fields, tree breeders have been forced to maintain a broad range of genotypes to cope with the extensive variation in local growing conditions (Owino, 1996). There is therefore much potential for more specific selection and breeding of tree genotypes for growth in the

more uniform conditions provided by agroforestry, so that the economic potential of the trees is maximised.

7.2.2 Choice of crop component species

The crop component of any agroforestry system is almost inevitably the species and cultivar best suited to the prevailing climatic conditions when grown as a sole crop. This choice might nevertheless be poorly adapted to the understorey microclimatic conditions experienced by the crops growing in agroforestry systems, particularly in semi-arid environments. For example, any delay in crop development resulting from modification of the thermal environment and increased soil water deficits within the crop rooting zone may make it necessary to adopt shorter duration varieties or species, especially in areas such as Machakos where consecutive cropping seasons are separated by only a few weeks. The greater incidence of water stress due to below-ground competition suggests that crop varieties which emerge and establish rapidly and have deep and extensive root systems would be better suited to compete more effectively for soil water and nutrients with the established root systems of the trees. However, such attributes may not be ideal during the tree establishment phase when severe competition from the crop may irreversibly alter the form and productive potential of the associated trees. A series of crop species or cultivars might therefore be recommended for different stages during the life of specific agroforestry systems. By characterising the understorey environment at each stage, it may be possible to identify crops or cultivars growing as sole stands in other areas where the environmental conditions are similar to those within the agroforestry system; these could then be adopted for use in specific agroforestry systems.

7.2.3 Management to promote greater productivity

This grevillea-based overstorey agroforestry system clearly demonstrated important interactions between the tree and crop components which favoured the crop during the tree establishment phase but switched in favour of the trees as the system matured. The degree to which these interactions are detrimental to system productivity depends largely on the size of the interface zone and hence the proportion of farmland that is affected.

The extent of the interface zone may be manipulated through pruning, planting arrangement and planting density.

Pruning the tree canopy represents a viable management option to limit competition between the tree and crop components of agroforestry systems and artificially encourage temporal complementarity. For example, pruning the canopy immediately prior to the cropping season reduces the quantity of water used by the trees during the initial stages of crop establishment and might also maintain favourable conditions for crop growth throughout the cropping season depending on the severity of the pruning regime. In areas of bimodal rainfall such as Machakos, pruning would be most appropriately timed to occur immediately prior to the season with most reliable rainfall, in order to minimise competition during the season when crop growth is potentially greatest; during the less reliable rainy season, the potential for crop growth is often limited by the erratic quantity and frequency of rainfall, to which the tree component is more resistant due to its extensive root system. Pruning the tree canopy represents a compromise between favouring crop growth and limiting tree productivity. However, there is scope to limit any detrimental impact on tree growth, while still providing a favourable understorey environment for crop growth. For example, it is conceivable that tree canopies with different shapes might transpire at similar rates but exhibit very different above-ground interactions with understorey crops. There is therefore a need to carry out agronomic-type trials to assess water use and productivity under various pruning regimes.

Brenner (1991) and Onyewotu *et al.* (1994) demonstrated that root pruning within the top 1 m of the soil profile may be used to limit competition between trees and crops. However, such a practice is highly labour-intensive and justifiable only if the productive potential of the tree is extremely attractive but the loss of crop productivity during the payback period (time between tree establishment and realisation of its productive potential) cannot be endured.

The inferior economic quality of grevillea grown in the agroforestry system, in conjunction with the severe suppression of understorey crop yields during the latter seasons, strongly suggests that the tree and crop components within this agroforestry system should be physically separated as far as possible and the interface zone kept to a

minimum. Howard (1997) and Corlett (1989) reached similar conclusions for semi-arid agroforestry systems containing leuceana/maize and leucaena/millet mixtures. However, as complete physical isolation of the two components is unlikely in the fields of smallholder subsistence farmers, the planting arrangement should take account of physical factors such as the prevailing wind direction, solar angle and slope, in addition to economic factors such as farm size to minimise the impact of the interface zone. This is particularly pertinent within the context of the rapidly rising rural populations and the resultant increase in pressure on rural resources. The density of trees in agroforestry systems might therefore have to be increased, making it necessary to plant trees away from the field boundaries and within the main body of the field, thereby increasing the overall size of the interface zone.

The planting densities of each component of agroforestry systems should be adjusted to maximise production and economic return. Indeed, in order to make meaningful comparisons of land equivalent ratios for sole and agroforestry systems, it is essential that each system is performing optimally (cf. Corlett, 1989). As agroforestry systems are generally associated with a long payback period, the productive capacity of the crop must be maintained as high as possible to support the farmer throughout this period. The crop component is therefore likely to continue to be planted at the optimum density for the sole crop and the tree at sub-optimal densities, even though this may not represent the most productive allocation of resources within the agroforestry system. There is considerable need for research into optimal system densities for the tree and crop components, and the extent to which these should be adjusted as the system matures.

7.2.4 Role of computer simulation modelling

Experimental research in agroforestry and the subsequent transfer of technology to farmers is severely hampered by the extended time periods required for agroforestry systems to establish and mature, particularly in dry environments. Consequently, the development of simulation models which provide quantitative assessments of the impact of different tree/crop combinations and management strategies on system productivity offers a means of rapidly screening potential agroforestry systems at greatly reduced cost. This would allow field trials to focus only on systems that have already been

identified as showing promise. However, the development of simulation models must adhere to two specific requirements:

Firstly, it is important that the number of parameters and level of detail required by the simulation model are easily defined by the intended end-user. Heavy reliance on published information will potentially undermine the reliability of simulations, while the need to conduct lengthy and intensive experimental campaigns to calibrate the models for individual species or environments would undermine the potential benefit of rapidity that such models provide. Extensive sensitivity analysis of model parameters should be conducted during model development to reduce the number of parameters to the minimum required.

Secondly, model development should be carried out in close association with intended end-users so that its structure and output are capable of meeting their requirements. For example, the annual time step adopted in HyPAR allows only one crop to be modelled during each year of the simulation and prevents tree growth from being output until the last day of the simulation. The model is therefore insufficiently flexible for end-users who wish to simulate the growth of different crops during the same simulation cycle, particularly in areas with bimodal rainfall, which are common in the semi-arid tropics, or to use model output to aid management decisions such as the timing of pruning.

As validation of model output against detailed experimental datasets is an essential element of model development, there is a genuine need for comprehensive datasets which provide high levels of information over extended periods, as was the case for the fieldwork described here. Validation exercises, such as the testing of HyPAR carried out during the current study, should ideally utilise datasets from a range of sites to assess the importance of variation in the prevailing environmental conditions. As a few such datasets already exist, there is considerable need for these to be made available in accessible formats so that model development may proceed effectively and rapidly.

BIBLIOGRAPHY

Adar, E.M., Gev, I., Lipp, J., Yakir, D., Gat, J. and Cohen, Y. (1995). Utilisation of oxygen-18 and deuterium in stem flow for the identification of transpiration sources: Soil water versus groundwater in sand dune terrain. Application of Tracers in Arid Zone Hydrology, **232**, 329-338.

Akyeampong, E., Hitimana, L., Franzel, S. and Munyemana, P.C. (1995). The agronomic and economic performance of banana, bean and tree intercropping in the highlands of Burundi: An interim assessment. Agroforestry Systems, **31**, 199-210.

Akyeampong, E. and Munyemana, P.C. (1993). Growth of *Grevillea robusta* at three densities and its influence on intercropped banana and beans. In: *AFRENA Burundi Project Report for the Period October 1991 to September 1992.* Akyeampong, E. (ed.). AFRENA Report No. 61. ICRAF, Nairobi.

Allen, S.J. (1990). Measurement and estimation of evaporation from soil under sparse barley crops in Northern Syria. Agricultural and Forest Meteorology, **49**, 291-309.

Allen, S.J. and Grime, V.L. (1995). Measurements of transpiration from savanna shrubs using sap flow gauges. Agricultural and Forest Meteorology, **75**, 23-41.

Allen, S.J., Hall, R.L. and Rosier, T.W. (1997). Transpiration of two poplar varieties grown as coppice for biomass production. Tree Physiology (submitted).

Alpizar, L., Fassbender, H.W., Heuveldop, J., Folster, H. and Enrichez, G. (1986). Modelling agroforestry systems of cacao (*Theobroma cacoa*) with laurel (*Cordia alliodora*) and poro (*Erithrina poeppigiana*) in Costa Rica. I. Inventory of organic matter and nutrients. Agroforestry Systems, **4**, 175-189.

Anderson, L.S., Muetzelfeldt, R.L. and Sinclair, F.L. (1993). An integrated research strategy for modelling and experimentation in agroforestry. Commonwealth Forestry Review, **72**, 166-174.

Anderson, L.S. and Sinclair, F.L. (1993). Ecological interactions in agroforestry systems. Agroforestry Abstracts, **6**, 57-91.

Anon (1897). *Grevillea robusta* in Ceylon in 1897. Tropical Agriculturist Supplement, Sep 1, p 216.

Azam-Ali, S.N. (1983). Seasonal estimates of transpiration from a millet crop using a porometer. Agricultural and Forest Meteorology, **30**, 13-24.

Azam-Ali, S.N., Gregory, P.J. and Monteith, J.L. (1984). Effects of planting density on water use and productivity of pearl millet (*Pennisetum typhoides*) grown on stored water. I. Growth of roots and shoots. Experimental Agriculture, **20**, 203-214.

Baker, J.M. and van Bavel, C.H.M. (1987). Measurements of the mass flow of water in the stems of herbaceous plants. Plant, Cell and Environment, **10**, 777-782.

Bell, J.P. (1987). *Neutron probe practice.* (Third Edition). Institute of Hydrology Report 19, Wallingford, Oxon, U.K.

Ben Salem, B. (1980). Arid-zone forestry: Where there are no forests and everything depends on trees. Unasylva, **32** (128), 16-18.

Ben Salem, B. and Palmberg, C. (1985). Place and role of trees and shrubs in dry areas. In: *Plants for Arid Lands.* Wickens, G.E., Goodin, J.R. and Field, D.V. (eds.). George Allen and Unwin, London, pp 93-102.

Bhatt, R.K., Misra, L.P. and Pathak, P.S. (1991). Diurnal variation in transpiration and energy exchange in some tree species from a semi-arid region. Range Management and Agroforestry, **12** (1), 79-84.

Black, C.R. and Ong, C.K. (1998). Utilisation of light and water in tropical agriculture. Agricultural and Forest Meteorology (in press).

Boland, D.J., Brooker, M.I.H., Chippendale, G.M., Hall, N., Hyland, B.P.M., Johnston, R.D., Kleinig, D.A. and Turner, J.D. (1984). *Forest Trees of Australia*, Nelson, CSIRO, Melbourne, 678 p.

Bolanos, J., Edmeades, G.O. and Martinez, L. (1993). Eight cycles of selection for drought tolerance in lowland tropical maize. III. Responses in drought adaptive physiological and morphological traits. Field Crops Research, **31**, 269-286.

Bradley, R.G. (1995). Modelling the growth and water use of tropical cereals in semi-arid environments. Ph.D. Thesis, The University of Nottingham, U.K.

Bradley, R.G. and Crout, N.M.J. (1994). *The PARCH model for predicting arable resource capture in hostile environments - User guide.* Tropical Crops Research Unit, The University of Nottingham, U.K., 122 p.

Brenner, A.J. (1991). *Tree-Crop Interactions Within a Sahelian Windbreak System.* Ph.D. Thesis, The University of Edinburgh, U.K., 284 p.

Brenner, A.J. (1996). Microclimatic modifications in agroforestry. In: *Tree-Crop Interactions: A Physiological Approach.* Ong, C.K. and Huxley, P. (eds.). CAB International, U.K., pp 159-188.

Brenner, A.J., Jarvis, P.G. and van den Beldt, R.J. (1995). Tree-crop interactions in a Sahelian windbreak system. 2. Growth response of millet in shelter. Agricultural and Forest Meteorology, **75**, 235-262.

Campbell, G.S. (1974). A simple method for determining unsaturated conductivity from moisture retention data. Soil Science, **117**, 311-314.

Campbell, G.S. (1985). Soil physics with BASIC. *Transport Models for Soil-Plant Systems*. Department of Agronomy and Soils, Washington State University, Elsevier Science Publishers.

Cannell, M.G.R. (1984). Woody biomass of forest stands. Forest Ecology and Management, **8**, 299-312.

Cannell, M.G.R. (1989). Physiological basis of wood production: A review. Scandinavian Journal of Forestry Research, **4**, 459-490

Cannell, M.G.R., Crout, N.M.J., Dewar, R.C., Lawson, G.J., Levy, P.E., Mobbs, D.C. and Robertson, W.H. (1994). *Agroforestry Modelling and Research Coordination Annual Report: June 1993 - June 1994.* Institute of Terrestrial Ecology, Penicuik, U.K.

Carberry, P.S., Muchow, R.C. and McCown, R.L. (1989). Testing the CERES-Maize simulation model in a semi-arid tropical environment. Field Crops Research, **20**, 297-315.

Cermak, J. and Kucera, J. (1987). Transpiration of mature stands of spruce (Picea albis (L.) Karst.) as estimated by the tree-trunk heat balance method. In: *Forest Hydrology and Watershed Management.* IAHS-AISH, **167**, 311-317.

Chapman, J.W. and Gower, S.T. (1991). Aboveground production and canopy dynamics in sugar maple and red oak trees in South Western Wisconsin. Canadian Journal of Forest Research, **21**, 1533-1543.

Child, R and Smith, A.N. (1960). Manganese toxicity in *Grevillea robusta.* Nature, **186**, 1087.

Coeloho, D.J. and Dale, R.F. (1980). An energy-crop growth variable for predicting corn growth and development: Planting to silking. Agronomy Journal, **72**, 503-510.

Coile, T.S. (1952). Soil and the growth of forests. Advances in Agronomy, **4**, 329-398.

Connor, D.J., Jones, T.J. and Palta, J.A. (1985). Response of sunflower to strategies of irrigation. II. Growth, yield and efficiency of water use. Field Crops Research, **10**, 15-26.

Coombes, J. and Hall, D.O. (1982). *Techniques in Bioproductivity and Photosynthesis*. Pergamon Press Ltd, Oxford, 171 p.

Cooper, P.J.M. (1979). The association between altitude, environmental variables, and maize growth and yield in Kenya. Journal of Agricultural Science, Cambridge, **93**, 635-649.

Cooper, P.J.M. and Law, R. (1978). Environmental and physiological studies of maize. *Maize Agronomy Research Project Final Report: Part 3, Vol. 1.* Kenyan Ministry of Agriculture, U.K. Overseas Development Administration, Eland House, Stag Place, London.

Cooper P.J.M., Keatinge, I.D.H. and Hughes, G. (1983). Crop evapotranspiration - a technique for calculation of its components by field measurements. Field Crops Research, **7**, 299-312.

Cooper, P.J.M., Gregory, P.J., Tully, D. and Harris, H.C. (1987). Improving water use efficiency of annual crops in rainfed farming systems of West Asia and North Africa. Experimental Agriculture, **23**, 113-158.

Corke, H. and Kannenberg, L.W. (1989). Selection for vegetative phase and actual filling period duration in short season maize. Crop Science **29**, 607-612.

Corlett, J.E. (1989). *Leuceana/Millet Alley Cropping in India: Microclimate and Productivity*. PhD Thesis, The University of Nottingham, U.K.

Corlett, J.E., Ong, C.K., Black, C.R. and Monteith, J.L. (1992a). Above- and below-ground interactions in a leuceana/millet alley cropping system. I. Experimental design, instrumentation and diurnal trends. Agricultural and Forest Meteorology, **60**, 53-72.

Corlett, J.E., Ong, C.K.O., Black, C.R. and Monteith, J.L. (1992b). Above- and below-ground interactions in a leuceana/millet alley cropping system. II. Light interception and dry matter production. Agricultural and Forest Meteorology, **60**, 73-91.

Cross and Zuber, (1972). Prediction of flowering dates in maize based on different methods of estimating thermal units. Journal of Agronomy, **64**, 351-355.

Daamen, C.C. and Simmonds, L.P. (1995). *Soil Water, Energy and Transpiration (SWEAT). A Numerical Model of Water and Energy Fluxes in Soil Profiles and Sparse Canopies.* Department of Soil Science, University of Reading, U.K.

Daynard, T.B. and Duncan, W.G. (1969). The black layer and grain maturity in corn. Crop Science, **9**, 473-476.

Denmead, O.T. (1984). Plant physiological methods for studying evapotranspiration: Problems of telling the forest from the trees. Agricultural Water Management, **8**, 167-190.

de Wit, C.T. (1958). Transpiration and Crop Yields. Versl. Landbouwk. Onderz, 64.6, Wageningen.

Duncan, W.G., Shaver, D.N. and Williams, W.A. (1973). Insolation and temperature effects on maize growth and yields. Crop Science, **13**, 187-190.

Eagleson, P.S. (1982). Ecological optimality in water limited natural soil-vegetation systems. 1. Theory and hypothesis. Water Resources Research, **18**, 325-340.

Early, E.B., McIlrath, W.O., Seif, R.D. and Hageman, R.H. (1967). Effects of shade applied at different stages of plant development on corn (*Zea mays* L.) production. Crop Science, 7, 151-156.

Ehleringer, J.R. (1989). Temperature and energy budgets. In: *Plant Physiological Ecology: Field Methods and Instrumentation.* Pearcy, R.W., Ehleringer, J., Mooney, H.A. and Rundel, P.W. (eds.). Chapman and Hall, London, pp 117-136.

Emechebe, A.M. and Shoyinka, S.A. (1985). Fungal and bacterial diseases of cowpea in Africa. In: *Cowpea: Research, Production and Utilisation.* Singh, S.R. and Rachie, K.O. (eds.). Wiley, New York.

Esegu, O.F.I. and Odoul, P.A. (1992). Baseline selection of *Grevillea robusta* in Western Kenya. In: *Grevillea robusta in Agroforestry Systems.* Harwood, C.E. (ed.). ICRAF, Nairobi. pp 183-188.

Evans, H.B.L. (1990). Forestry extension in EMI districts, Kenya. Commonwealth Forestry Review, **69**, 309-312.

Falkenmark, M. (1996). Meeting the water requirements of an expanding world population. In: *Land Resources; On the Edge of a Malthusian Precipice.* Greenland, D.J., Gregory, P.J. and Nye, P.H. (eds.). Royal Society, CAB International, Wallingford, Oxon, U.K., pp 69-76.

FAO, 1994. *Annual Production Yearbook: Volume 47.* FAO Statistics Series No. 117. Food and Agriculture Organisation of the United Nations.

Farnsworth, K.D. and van Gardingen, P.R. (1995). Allometric analysis of sitka spruce branches - mechanical versus hydraulic design principles. Trees - Structure and Function **10**, 1-12.

Fichtner, K. and Schultz, E.-D. (1990). Xylem water flow in tropical vines as measured by a steady state heating method. Oecologia, **82**, 355-361.

Fischer, G. and Heilig, G.K. (1996). Population momentum and the demand on land and water resources. In: *Land Resources; On the Edge of a Malthusian Precipice.* Greenland, D.J., Gregory, P.J. and Nye, P.H. (eds.). Royal Society, CAB International, Wallingford, Oxon, U.K., pp 2-29.

Fischer, K.S. and Palmer, A.F.E. (1984). Tropical maize. In: *The Physiology of Tropical Field Crops.* Goldsworthy, P.R. and Fisher, N.M. (eds.). John Wiley and Sons, Chichester, U.K., pp 213-248.

Fischer, R.A. and Turner, N.C. (1978). Plant productivity in the arid and semi-arid zones. Annual Review of Plant Physiology, **29**, 277-317.

Flanagan, L.B., Ehlringer, J.R. and Marshall, J.D. (1992). Differential uptake of summer precipitation in co-occurring trees and shrubs in a pinyon-juniper woodland. Plant, Cell and Environment, 15, 831-836.

Foley, G. (1987). *The Energy Question.* Penguin, London, 320 p.

Fownes, J.H. and Harrington, R.H. (1990). Modelling growth and optimal rotations of tropical multipurpose trees using unit leaf rate and leaf area index. Journal of Applied Ecology **27**, 886-896.

Friend, A.D., Stevens, A.K., Knox, R.G. and Cannell, M.G.R. (1997). A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid v3.0). Ecological Modelling, **95**, 249-287.

Gallagher, J.N. (1979). Field studies of cereal leaf growth: Initiation and expansion in relation to temperature ontogeny. Journal of Experimental Botany, **30**, 625-636.

Garcia-Huidobro, J., Monteith, J.L. and Squire, G.R. (1982). Time, temperature and germination of pearl millet (*Pennisetum typhoides* S & H). 1. Constant temperature. Journal of Experimental Botany, **33**, 288-296.

Gates, P.J. and Brown, K. (1988). *Acacia tortilis* and *Prosopis cineraria*: Leguminous trees for arid areas. Outlook on Agriculture, **17** (2), 61-64.

Gindel, I. (1973). *The New Ecophysical Approach to Forest-Relationships in Arid Climates*. Junk, The Hague, Netherlands, 142 pp.

Goudie, A. (1986). *The Human Impact on the Natural Environment.* Basil Blackwell, Oxford, U.K., 338 p.

Green, S.R. and Clothier, B.E. (1988). Water use of kiwifruit vines and apple trees by the heat-pulse technique. Journal of Experimental Botany, **39**, 115-123.

Gregson, K., Hector, D.G., and McGowan, M. (1987). A one-parameter model for determining soil water characteristics. Journal of Soil Science, **38**, 483-486.

Grime, J.P. (1974). Vegetation classification by reference to strategies. Nature, **250**, 26-30.

Groot, A. and King, K.M. (1992). Measurement of sap flow by the heat balance method: Numerical analysis and application to coniferous seedlings. Agricultural and Forest Meteorology, **59**, 289-308.

Grout, T.G. and Richards, G.I. (1990). The influence of windbreak species on citrus thrip (*Thysanoptera thripidae*) populations and their damage to South African citrus orchards. Journal of the Entomology Society of South Africa, **53**, 151-158.

Guinard, Y., Hitimana, L., Franzel, S. and Akyeampong, E. (1992). *Complement de Diagnostic Agro-Forestier dans la Region Naturelle du Kirimiro.* AFRENA Report No. 66, ICRAF, Nairobi.

Hall, R.L. and Allen, S.J. (1997). Water use of poplar clones grown as short-rotation coppice at two sites in the United Kingdom. Aspects of Applied Biology, **49**, 163-172.

Hall, A.E. and Patel, P.N. (1985). Breeding for resistance to drought and heat. In: *Cowpea: Research, Production and Utilisation.* Singh, S.R. and Rachie, K.O. (eds.). Wiley, New York.

Hall, A.J., Vilella, A., Trapani, N. and Chimenti, C. (1982). The effects of water stress and genotype on the dynamics of pollen-shedding and silking in maize. Field Crops Research, **5**, 349-363.

Ham, J.M., Heilman, J.L. and Lascano, R.J. (1990). Determination of soil water evaporation and transpiration from energy balance and stem flow measurements. Agricultural and Forest Meteorology, **52**, 287-301.

Harsh, L.N., Tewari, J.C. and Puri, S. (1993). Agroforestry in arid regions of India. In: *Agroforestry in South Asia: Problems and Applied Research Perspectives.* Bentley, W.R., Khosla, P.K. and Seckler, K. (eds.). Winrock-Oxford and IBH series, USA and India.

Harwood, C.E. (1989). *Grevillea robusta: An Annotated Bibliography.* ICRAF, Nairobi.

Harwood, C.E. (ed.) (1992). *Grevillea robusta in Agroforestry Systems: Proceedings of an International Workshop.* ICRAF, Nairobi.

Harwood, C.E. and Getahun, A. (1990). Australian tree finds success in Africa. Agroforestry Today, **2** (1), 5-8.

Harwood, C.E. and Owino, F. (1992). Design of a genetic improvement strategy for Grevillea robusta. In: *Grevillea robusta in Agroforestry Systems: Proceedings of an International Workshop.* Harwood, C.E. (ed.). ICRAF, Nairobi, pp 141-150.

Hatton, T.J. and Vertessey, R.A. (1989). Variability of sap flow in a Pinus radiata plantation and the robust estimation of transpiration. *Hydrology and Water Resources Symposium*, Christchurch, New Zealand, 6 October.

Hatton, T.J. and Vertessey, R.A. (1990). Transpiration of plantation *Pinus radiata* estimated by the heat pulse method and the Bowen Ratio. Hydrological Processes, **4,** 289-298.

Hatton, T.J. and Wu, H.I. (1995). Scaling theory to extrapolate individual tree water use to stand water use. Hydrological Processes, **9,** 527-540.

Hawkins, R.C. and Cooper, P.J.M. (1981). Growth, development and grain yield of maize. Experimental Agriculture, **17,** 203-208.

Hess, T.M. and Stevens, W. (1994). *An Evaluation of the PARCH Model for Simulating Maize Yield in the Arid and Semi-Arid Lands of Kenya.* KARI-Silsoe College Linkage Project, 28 February- 4 March 1994. Silsoe College, Cranfield University, U.K., 36 p.

Hinman, C.W. and Hinman, J.W. (1992). *The Plight and Promise of Arid Land Agriculture.* Columbian University Press, New York, 253 p.

Hoekstra, D., Aluma, J., Thijssen, H., Muwanga, J. and Sekalye, I.B. (1991). *Diagnostic Study of Banana-Tree Associations in the Intensive Banana-Coffee Lakeshore System, Uganda.* AFRENA Report 44. ICRAF, Nairobi.

Howard, S.B. (1997). *Resource Capture and Productivity of Agroforestry Systems in Kenya.* Ph.D. Thesis, The University of Nottingham, U.K.

Howard, S.B., Ong, C.K., Black, C.R., Khan, A.A.H. (1997). Using sap flow gauges to quantify water uptake by tree roots from beneath the crop rooting zone in agroforestry systems. Agroforestry Systems, **35,** 15-29.

Huxley, P.A., Pinney, A. and Gutama, D. (1989). *Development of Agroforestry Research Methodology Aimed at Simplifying the Study of Potential Tree/Crop Mixtures.* Final Report, Project No. 1-432-60005613, ICRAF, Nairobi, 109 p.

Huxley, P.A., Pinney, A., Akunda, E. and Muriya, P. (1994). A tree/crop interface orientation experiment with a *Grevillea robusta* hedgerow and maize. Agroforestry Systems, **26**, 23-45.

International Centre for Research in Agroforestry (1994). *Annual Report 1993.* ICRAF, Nairobi. ISBN 92 9059 111 8, 208 p.

International Centre for Research in Agroforestry (1995). *Annual Report 1994.* ICRAF, Nairobi. ISBN 92 9059 121 8, 239 p.

International Centre for Research in Agroforestry (1996). *Annual Report 1995.* ICRAF, Nairobi. ISBN 92 9059 1226, 288 p.

Ishida, T., Campbell, G.S. and Calissendorff, C. (1991). Improved heat balance method for determining sap flow rate. Agricultural and Forest Meteorology, **56**, 35-48.

Jackson, J.E. (1989). Tree and crop selection and management to optimise overall system productivity, especially light utilisation, in agroforestry. In: *Meteorology and Agroforestry*. Reifsnyder, W.S. and Darnhofer, T.O. (eds.). ICRAF, Nairobi.

Jackson, N.A. and Wallace, J.S. (1998). Soil evaporation in a *Grevillea robusta* agroforestry system. I. Use of microlysimeters to measure soil evaporation. Agricultural and Forest Meteorology (submitted).

Jackson, N.A., Wallace, J.S., Smith, D.M. and Roberts, J.M. (1997). *Water Balance of Agroforestry Systems on Hillslopes - Phase II.* Annual Report to DFID Forestry Research Programme, Institute of Hydrology, Wallingford, U.K., 11 p.

Jarvis, P.G. and McNaughton, K.G. (1986). Stomatal control of transpiration: Scaling up from leaf to region. Advances in Ecological Research, **15**, 1-49.

Jones, C.A. and Kiniry, J.R. (1986). *CERES-Maize: A Simulation Model of Maize Growth and Development.* Texas A&M University Press, U.S.A., 194 p.

Jones, H.G. (1992). *Plants and Microclimate: A Quantitative Approach to Environmental Plant Physiology.* Second edition. Cambridge University Press, Cambridge, UK.

Jones, R.J., Roessler, J. and Ouattar, S. (1985). Thermal environment during endosperm cell division in maize: effects on number of endosperm cells and starch granules. Crop Science, **25**, 830-834.

Jonsson, K. (1995). *Agroforestry in Dry Savanna Areas in Africa: Interactions Between Trees, Soils and Crops.* PhD Thesis, Swedish University of Agricultural Sciences, Umea, Sweden.

Jonsson, K., Fidjeland, L., Maghembe, J.A., and Hogberg, P. (1988). The vertical distribution of fine roots of five tree species and maize in Morogoro, Tanzania. Agroforestry Systems, **6**, 63-69.

Jordan, W.R. (1983). Whole plant response to water deficits: An overview. In: *Limitations to Efficient Water Use in Crop Production.* Taylor, H.M., Jordan, W.R. and Sinclair, T.R. (eds.). ASA-CSSA-SSSA, Madison, USA, pp 289-317.

Kallinganire, A and Hall, J.B. (1993). Growth and biomass production of young *Grevillea robusta* provenances in Rwanda. Forest Ecology and Management, **62**, 73-84.

Kanemasu, E.T. (1983). Yield and water-use relationships: Some problems of relating grain yield to transpiration. In: *Limitations to Efficient Water Use in Crop Production.* Taylor, H.M., Jordan, W.R. and Sinclair, T.R. (eds.). ASA-CSSA-SSSA, Madison, USA, pp 413-417.

Keane, M. and Weetman, G.F. (1987). Leaf area-sapwood cross-sectional area relationships in repressed stands of lodgepole pine. Canadian Journal of Forest Research, 17, 205-209.

Keating, B.A. and Carberry, P.S. (1993). Resource capture and use in intercropping: Solar radiation. Field Crops Research, 34, 273-302.

Keating, B.A., Wafula, B.M., Poulton, P.L. and Hargreaves, J.N.G. (1993). *CMKEN-Maize V6.0: A Crop Simulation Model for Maize - User Manual.* ACIAR/CSIRO.

Khalifa, F.M. and Ong, C.K. (1990). Effect of supra-optimal temperatures on germination of pearl millet (*Pennisetum glaucum* (L) R.BR) hybrids. Annals of Arid Zone Research, 29, 279-288.

Khan, A.A.H. and Ong, C.K. (1995). Correction of systematic errors in estimates of transpiration obtained using a constant temperature heat balance technique. Experimental Agriculture, 31, 461-472.

Kibe, J.M., Ochung, H. and Macharia, P.N. (1981). *Soils and Vegetation of the ICRAF Experimental Farm (Machakos District).* Kenyan Ministry of Agriculture Soil Survey. Report No. D23, 68 p.

Kiepe, P. (1995). *No Runoff, No Soil Loss.* PhD Thesis, Wageningen Agricultural University, The Netherlands, 156 p.

Kilewe, A.M. and Ulsaker, L.G. (1984). Topographical modification of land to concentrate and redistribute runoff for crop production. East African Agriculture and Forestry Journal, 44, 257-265.

King, D.A. (1996). Allometry and life-history of tropical trees. Journal of Tropical Ecology, 12, 25-44.

Kiniry, J.R., Jones, C.A., O'Toole, J.C., Blanchet, R., Cabelguenne, M. and Spanel, D.A. (1989). Radiation-use efficiency in biomass accumulation prior to grain filling for five grain crop species. Field Crops Research, 20, 51-64.

Kozlowski, T.T. (1964). *Shoot growth in woody plants*. Botanical Reviews, 30, 335.

Kushalapa, K.A. (1988). Silvicultural systems in the tropical rain forests of Karnataka, India. Indian Forester, 114, 372-378.

Ladefoged, K. (1963). Transpiration of forest trees in closed stands. Physiologia Plantarum, 16, 378-414.

Lamont, B. (1982). Mechanisms for enhancing nutrient uptake in plants with particular reference to the Mediterranean, South Africa and Western Australia. Botanical Reviews, 48, 597-689.

Lange, O.L., Kappen, L. and Schulze, E.-D. (1976). Water and plant life. Ecological Studies 19. Springer Verlag, Berlin.

Langstrom, B. and Hellqvist, C. (1991). Effects of different pruning regimes on growth and sapwood area of Scots pine. Forest Ecology and Management, 44, 239-254.

Lawson, G.J., Cannell, M.G.R., Mobbs, D.C., Crout, N.M.J., Muetzelfeldt, R., Wallace, J.S., Gregory, P.J., Thomas, T.H., Jagtap, S., Ludlow, A.R., Cobbina, J., Arah, J., MacDonald, K.J., Taylor, J., Sharp, L., Wiggins, G., Flynn, L., Livesley, S., Willis, R.W. and Friend, A.D. (1996). *Agroforestry Modelling and Research Coordination Annual Report: June 1995-May 1996.* Institute of Terrestrial Ecology, Penicuik, U.K., 178 p.

Laycock, D.H. and Wood, R.A. (1963). Some observations of soil moisture use under tea in Nyasaland. II. The effects of shade trees. Tropical Agriculture (Trinidad), 40, 42-48.

Lenga, F.K. and Keating, B.A. (1990). Use of thermal time to predict phenology of Kenyan maize germplasm. East African Agriculture and Forestry Journal, **55**, 103-123.

Lomnicki, A. (1988). The place of modelling in ecology. Oikos, **52**, 139-142.

Loomis, R.S. and Connor, D.J. (1992). *Crop Ecology: Productivity and Management in Agricultural Systems*. Cambridge University Press, U.K., 600p

Lott, J.E., Khan, A.A.H., Ong, C.K. and Black, C.R. 1996. Sap flow measurements of lateral roots in agroforestry systems. Tree Physiology, **16**, 995-1001.

Lott, J.E., Black, C.R. and Ong, C.K. (1997). *Resource Utilisation by Trees and Crops in Agroforestry Systems*. Final report on Project R5810 to DFID, The University of Nottingham, U.K., 81 p.

Lott, J.E., Black, C.R. and Ong, C.K. (1998). Allometric estimation of above-ground biomass and leaf area in managed *Grevillea robusta* agroforestry systems. Tree Physiology (submitted).

Ludlow, M.M. and Muchow, R.C. (1990). A critical evaluation of traits for improving crop yields in water limited environments. Advances in Agronomy, **43**, 107-153.

Lugo, A.E., Gonzalez-Liboy, J.A., Contron, B. and Digger, K. (1978). Structure, productivity, and transpiration of a subtropical dry forest in Puerto Rico, **10**, 278-291.

Lyamchai, C.J., Gillespie, T.J. and Brown, D.M. (1997). Estimating maize yield in northern Tanzania by adapting SIMCOY, a temperate-zone simulation model. Agricultural and Forest Meteorology, **85**, 75-86.

MacKerron, D,K.L. (1976). Wind damage to the surface of strawberry leaves. Annals of Botany, **40**, 351-354.

Madan, R.N. and Tandon, B. (1991). Utilisation of some plantation, agroforestry and social forestry species for the production of dissolving pulps. Indian Forester, **117**, 29-36.

Margolis, H.A., Gagnon, R.R., Pothier, D. and Pineau, M. (1988). The adjustment of growth, sapwood area, heartwood area, and sapwood saturated permeability of balsam fir after different intensities of pruning. Canadian Journal of Forest Research, **18**, 23-27.

Marshall, F.M. (1995). *Resource Partitioning and Productivity of Perennial Pigeonpea/Groundnut Agroforestry Systems in India.* Ph.D. Thesis, The University of Nottingham, U.K.

Massman, W.J. (1992). A surface-energy balance method for partitioning evapotranspiration data into plant and soil components for a surface with partial canopy cover. Water Resources Research, **28** (6), 1723-1732.

McIntyre, B.D., Flower, D.J. and Riha, S.J., (1993). Temperature and soil water effects on radiation use and growth of pearl millet in a semi-arid environment. Agricultural and Forest Meteorology, **66**, 211-227.

McIntyre, B.D., Riha, S.J. and Ong, C.K. (1996). Light interception and evapotranspiration in hedgerow agroforestry systems. Agricultural Forest Meteorology, 81, 31-40.

McNaughton, K.G. (1988). Effects of windbreaks on turbulent transport and microclimate. Agriculture, Ecosystems and Environment, **22**, 17-39.

McPhearson, H.G. and Slatyer, R.O. (1973). Mechanisms regulating photosynthesis in *Pennisetum typhoides*. Australian Journal of Biological Sciences, 26 329-339.

Meinzer, F.C., Fownes, J.H. and Harrington, R.A. (1996). Growth indicies and stomatal control of transpiration in *Acacia koa* stands planted at different densities. Tree Physiology, **16**, 607-615.

Mencuccini, M. and Grace, J. (1995). Climate influences the leaf-area sapwood area ratio in Scots pine. Tree Physiology, **15**, 1-10.

Miller, P.C. and Poole, D.K. (1979). Patterns of water use by shrubs in Southern California. Forest Science, **25** (1), 84-98.

Mobbs, D.C. and Cannell, M.G.R. (1995). Preliminary results from a regional simulation demonstrating the use of HyPAR V1.0. In: *Agroforestry Modelling and Research Co-ordination Annual Report, June 1994-June 1995.* Lawson, G.J., Mobbs, D.C., Crout, N.M.J., Levy, P.E., Wallace, J.S., Gregory, P.J., MacDonald, K.J., Thomas, T.H., Cannell, M.G.R., Bradley, R.G., McIver, H.L. and van Gestel, N.C.G (eds.). Institute of Terrestrial Ecology, Penicuik, U.K., 113 p.

Mohamed, H.A., Clark, J.A. and Ong, C.K. (1988). Genotypic differences in the temperature responses of tropical crops. Journal of Experimental Botany, **39**, 1121-1128.

Monteith, J.L. (1977). Climate. In: *Ecophysiology of Tropical Crops.* Alvim, P. de T. and Kozlowski, T.T. (eds.). Academic Press, London, pp 1-27.

Monteith, J.L. (1981). Evaporation and surface temperature. Quarterly Journal of the Royal Meteorological Society,**107**, 1-27.

Monteith, J.L. (1988). Steps in crop climatology. In: *Challenges in Dryland Agriculture: A Global Perspective. Proceedings of the International Conference on Dryland Farming,* August 1988. Unger, P.W., Sneed, T.V., Jordan, W.R. and Jensen, R. (eds.). Texas Agricultural Experimental Station, Texas, U.S.A., pp 273-282.

Monteith, J.L. (1990). Conservative behaviour in the response of crops to water and light. In: *Theoretical Production Ecology: Reflections and Prospects.* Rabbinge, R., Goudriaan, J., van Keulen, H., Penning de Vries, F.W.T. and van Laar, H.H. (eds.). Pudoc, Wageningen, pp 3-16.

Monteith, J.L. (1993). *Using Tube Solarimeters to Measure Radiation Intercepted by Crop Canopies and to Analyse Stand Growth.* Applications Note TSL-AN-4-1, Delta-T Devices, Cambridge, U.K., 11 p.

Monteith, J.L. (1996). The quest for balance in crop modelling. Agronomy Journal, **88**, 695-697.

Monteith, J.L., Gregory, P.J., Marshall, B, Ong, C.K., Saffell, R.A. and Squire, G.R. (1981). Physical measurements in crop physiology. I. Growth and gas exchange. Experimental Agriculture, **17**, 113-126.

Monteith, J.L., Ong, C.K. and Corlett, J.E. (1991). Microclimatic interactions in agroforestry systems. Forest Ecology and Management, **45**, 31-44.

Monteith, J.L. and Virmani, S.M. (1991). Quantifying climatic risk in the semi-arid tropics. In: *Climatic Risk in Crop Production: Models and Management for the Semi-Arid Tropics and Subtropics.* Muchow, R.C. and Bellamy, J.A. (eds.). CAB International, Wallingford, Oxon, U.K.

Muchow, R.C. (1989). Comparative productivity of maize, sorghum and pearl millet in a semi-arid tropical enivironment. II. Effect of water deficits. Field Crops Research, **20**, 207-219.

Muchow, R.C. (1990). Effects of high temperature on grain growth in field grown maize. Field Crops Research, **23**, 145-158.

Muchow, R.C. and Davis, R. (1988). Effect of nitrogen supply on the comparative productivity of maize and sorghum in a semi-arid tropical environment. II. Radiation interception and biomass accumulation. Field Crops Research, **18**, 17-30.

Mwihomeke, S.T. (1992). A comparative study of the rooting depth of *Grevillea robusta* interplanted with sugar-cane along contour strips. In: *Grevillea robusta in Agroforestry Systems: Proceedings of an International Workshop*. Harwood, C.E. (ed.). ICRAF, Nairobi, pp 117-124.

Natarajan, K., Paliwal, K. and Gnanam, A. (1988). Biomass and leaf area relationships in *Leucaena leucocephala* (Lam.) de Wit. Photosynthetica, **22**, 105-107.

Nautiyal, S., Badola, H.K., Pal, M. and Negi, D.S. (1994). Plant responses to water stress: Changes in growth, dry matter production, stomatal frequency and leaf anatomy. Biologia Plantarum, **36**, 91-97.

Nemani R.R. and Running, S.W. (1989). Testing a theoretical climate-soil-leaf area hydologic equilibrium of forests using satellite data and ecosystem simulation. Agricultural and Forest Meteorology, 44, 245-260.

Nicholas, I.D. (1988). Plantings in tropical and subtropical areas. Agriculture, Ecosystems and Environment, **22-23**, 465-482.

Norman, M.J.T., Pearson, C.J. and Searle, P.G.E. (1984). *The Ecology of Tropical Food Crops*. Cambridge University Press, Cambridge, U.K., 358 pp.

Nygren, P., Rebottaro, S. and Chavarría, R. (1993). Application of the pipe model theory to non-destructive estimation of leaf biomass and leaf area of pruned agroforestry trees. Agroforestry Systems, **23**, 63-77.

Olbrich, B.W., Le Roux, D., Poulter, A.G., Bond, W.J. and Stock, W.D. (1993). Variation in water use efficiency and ^{13}C levels in *Eucalyptus grandis* clones. Journal of Hydrology, **150**, 615-633.

Omoro, L.M.A. and Nair, P.K.R. (1993). The effects of mulching with multi-purpose-tree prunnings on soil and water run-off under semi-arid conditions in Kenya. Agroforestry Systems, **22**, 225-239.

Ong, C.K. (1983). Response to temperature in a stand of pearl millet (*Pennisetum typhoides* S & H). 1. Constant temperature. Journal of Experimental Botany, **34**, 322-336.

Ong, C.K. (1995). Current process-level research and modelling at ICRAF. In: *Proceedings of Agroforestry Modelling Workshop, Newbattle Abbey, Edinburgh 19-20 January 1995.* Lawson, G.J. and McIver, H.W. (eds.). Institute of Terrestrial Ecology, Penicuik, U.K., 57 p.

Ong, C.K. and Black C.R. (1994). Complementarity in resource use in intercropping and agroforestry systems. In: *Resource Capture by Crops.* Monteith, J.L., Scott, R.K. and Unsworth, M.H. (eds.). Nottingham University Press, U.K., pp 255-278.

Ong, C.K., Black, C.R., Marshall, F.M. and Corlett, J.E. (1996). Principles of resource capture and utilisation of light and water. In: *Tree-Crop Interactions: A Physiological Approach.* Ong, C.K. and Huxley, P. (eds.). CAB International, Wallingford, U.K. and ICRAF, Nairobi, pp 73-158.

Ong, C.K. and Khan, A.A.H. (1993). The direct measurement of water uptake by individual tree roots. Agroforestry Today, **5**, 2-5.

Ong, C.K. and Monteith, J.L. (1984). Response of pearl millet to light and temperature. In: *Agrometeorology of Sorghum and Millet in the Semi-Arid Tropics. Proceedings of the International Symposium.* Virmani, S. and Sivakumar, M. (eds.). ICRISAT, India.

Ong, C.K. and Monteith, J.L. (1985). Response of pearl millet to light and temperature. Field Crops Research, **11**, 141-160.

Ong, C.K., Odongo, J.C.W., Marshall, F.M. and Black, C.R. (1992). Water use of agroforestry systems in semi-arid India. In: *Growth and Water Use of Forest Plantations.* Calder, I.R., Hall, R.L. and Adlard, P.G. (eds). Wiley, Chichester, U.K., pp 347-358.

Ong, C.K. and Squire, G.R. (1984). Responses to temperature in a stand of pearl millet (*Pennisetum typhoides* S. & H.). VII. Final number of spikelets and grains. Journal of Experimental Botany, 35, 1233-1240.

Ongugo, P.O. (1992). Place of *Grevillea robusta* in national agroforestry and wood production policies and plans. In: Grevillea robusta *in Agroforestry Systems.* Harwood, C.E. (ed.). ICRAF, Nairobi.

Onyewotu, L.O.Z., Ogigirigi, M.A. and Stigter, C.J. (1994). A study of the competitive effects of *Eucalyptus camendulensis* shelterbelts and an adjacent millet (*Pennisetum typhoides*) crop. Agriculture Ecosystems and Environment, 51, 281-286.

Othieno, C.D. (1983). Studies on the use of shade in tea plantations in Kenya. I. Effect on nutrient uptake and yield of tea - preliminary results. Tea, 4 (2), 13-20.

Ovalle, C. and Avendano, J. (1987). Interactions of the tree layer with the herbaceous understory layer in the plant-communities of *Acacia caven* in Chilli. 1. Tree influence on the botanical composition, production and phenology of the herbaceous stratum. Acta-Oecologia, 8 (4), 385-404.

Owino, F. (1996). Selection for adaptation in multipurpose trees and shrubs for production and function in agroforestry systems. Euphytica, 92, 225-234.

Owuor, P.O., Othieno, C.O., Howard, G.E., Robinson, J.M. and Cooke, R.D. (1988). Studies on the use of shade in tea plantations in Kenya: The effects on chemical composition and quality of made tea. Journal of Science Food and Agriculture, 46, 63-70.

Ozier-Lafontaine, H., Vercambre, G. and Tournebize, R. (1997). Radiation and transpiration partitioning in a maize-sorghum intercrop. Test and evaluation of two models. Field Crops Research, 49, 127-145.

Pate, J.S. and Farquar, G.D. (1988). Role of the crop plant in the cycling of nitrogen. In: *Advances in Nitrogen Cycling in Agricultural Systems.* J.R. Wilson (ed.). CAB International, Wallingford, U.K., pp 23-45.

Pearcy, R.W., Ehleringer, J., Mooney, H.A. and Rundel, P.W. (eds.) (1989). *Plant Physiological Ecology: Field Methods and Instrumentation.* Chapman and Hall, London, 457 p.

Peden, DG, Okorio, J and Wajja-Musukwe, N. (1996). Commercial pole production in linear agroforestry systems. Agroforestry Systems, 33, 177-186.

Pellerin, S. and Pages, L. (1994). Evaluation of parameters describing the root system architecture of field grown maize plants. I. Elongation of seminal and nodal roots and extension of their branched zone. Plant and Soil, 164, 155-167.

Peltier, J.P., Carlier, G., El-Aboudi, A. and Douche, B. (1990). Plant water relations of the argan tree (*Argania spinosa*) in an arid climate under oceanic influence (the Sous Plain, Morocco). Acta-Oecolgia, 11, 643-668.

Penning de Vries, F.W.T. and Spitters, C.J.T. (1991). The potential for improvement in crop yield simulation. In: *Climatic Risk and Crop Production: Models and Management for the Semi-arid Tropics.* Muchow, R.C. and Bellamy, J.A. (eds.). CAB International, Wallingford, U.K., pp 123-140.

Pilbeam, C.J. and Warren, G.P. (1995). Use of ^{15}N for fertilizer N recovery and N mineralization studies in semi-arid Kenya. Fertilizer Research, 42, 123-128.

Pilbeam, C.J., Wood, M. and Mugane, P.G. (1995). Nitrogen use in maize-grain legume cropping systems in semi-arid Kenya. Biological Fertilisation of Soils, **20,** 57-62.

Purseglove, J.W. (1972). *Tropical Crops: Monocotyledons.* Longman, London.

Rachie, K.O. (1985). Introduction. In: *Cowpea: Research, Production and Utilisation.* Singh, S.R. and Rachie, K.O. (eds.). Wiley, New York.

Ralston (1964). Estimation of forest site productivity. International Review of Forestry Research, **1,** 171.

Rao, M.R. and Coe, R. (1992). Evaluating the results of agroforestry research. Agroforestry Today, **4** (1), 4-9.

Rennolls, K. (1994). Pipe-model theory of stem-profile development. Forest Ecology and Management, **69,** 41-55.

Ritchie, J.T. (1991). Specifications for the ideal model for predicting crop yields. In: *Climatic Risk and Crop Production: Models and Management for the Semi-arid Tropics.* Muchow, R.C. and Bellamy, J.A. (eds.). CAB International, Wallingford, U.K.

Robertson, M.J., Fukai, S., Ludlow, M.M., and Hammer, G.L. (1993). Water extraction by grain sorghum in a sub-humid environment. I. Analysis of the water extraction pattern. Field Crops Research, 33, 81-97.

Rosenberg, N.J. (1984). The role of the meteorologist and climatologist in improving food production capabilities in semi-arid regions. In: *Agrometeorology of Sorghum and Millet in the Semi-Arid Tropics. Proceedings of the International Symposium.* Virmani, S. and Sivakumar, M. (eds.). ICRISAT, India, pp 21-29.

Rosenberg, N.J., Blad, B.L. and Verma, S.B. (1983). *Microclimate: The Biological Environment.* John Wiley and Sons, New York, 495 p.

Rutter, A.J. (1968). Water consumption by forests. In: *Water Deficits and Plant Growth Vol. II. Plant Water Consumption and Response.* Kozlowski, T.T. (ed.). Academic Press, New York and London, pp 23-84.

Sakuratani, T. (1987). Studies on evapotranspiration from crops. 2. Separate estimation of transpiration and evaporation from a soybean field without water shortage. Journal of Agricultural Meteorology, 42, 309-317.

Sakuratani, T. (1990). Measurement of sap flux rate in stems of rice plants. Agricultural Meteorology, 45, 277-280.

Salisbury, F.B. and Ross, C.W. (1992). *Plant Physiology.* Wadsworth Biology Series, Belmont, C.A., U.S.A., 682 p.

Sanchez, P.A., Buresh, R.J. and Leaky, R.R.B. (1996). Trees, soil and food scarcity. In: *Land Resources; On the Edge of a Malthusian Precipice.* Greenland, D.J., Gregory, P.J. and Nye, P.H. (eds.). Royal Society, CAB International, Wallingford, Oxon, U.K., pp 89-101.

Scholes, M.C., Swift, M.J., Heal, O.W., Sanchez, P.A., Ingram, J.S.I. and Dalal, R. (1994). Soil fertility research in response to the demand for sustainability. In: *The Biological Management of Tropical Soil Fertility.* Woomer, P.L. and Swift, M.J. (eds.). John Wiley and Sons, Chichester.

Scott, R.M., Webster, R. and Lawrence, C.J. (1971). *A Land System Atlas of Western Kenya.* Christchurch, Hampshire, U.K.

Schulze, E.-D., Cermak, J., Mtyssek, R., Penka, M., Zimmermann, R., Vasicek, F., Gries, W. and Kucera, J. (1985). Canopy transpiration and water fluxes in the xylem of the trunk of *Larix* and *Picea* trees - a comparison of xylem flow, porometer and cuvette measurements. Oecologia, **66**, 475-483.

Senock, R.S. and Ham, J.M. (1993). Heat balance sap flow gauge for small diameter stems. Plant, Cell and Environment, **16**, 593-601.

Sestak, Z., Catsky, J. and Jarvis, P.G. (1971). *Plant Photosynthetic Production: Manual of Methods*. Junk, The Hague, Netherlands, 800 p.

Siemer, E.G., Leng, E.R. and Bonnett, O.T. (1969). Timing and correlation of major development events in maize, *Zea mays* L. Agronomy Journal, **61**, 14-17.

Sharma, R.A. (1992). Agro-forestry in India. Indian Forester, **118**, 191-201.

Shinozaki, K., Yoda, K., Hozumi, K. and Kira, T. (1964). A quantitative analysis of plant form: The pipe model theory. II. Further evidence of the theory and its application in forest ecology. Japanese Journal of Ecology, **14**, 133-139.

Sivakumar, M. V. K., Huda, A.K.S. and Virmani, S.M. (1984). Physical environment of sorghum and millet growing areas in South Asia. In: *Agrometerology of Sorghum and Millet in the Semi-Arid Tropics. Proceedings of the International Symposium.* Virmani, S. and Sivakumar, M. (eds.). ICRISAT, India.

Skene, K.R., Kierans, M., Sprent, J.I. and Raven J.A. (1996). Structural aspects of cluster root development and their possible significance for nutrient acquisition in *Grevillea robusta* (Proteaceae). Annals of Botany, **77**, 443-451.

Smith, D.M. (1995). *Water Use by Windbreak Trees in the Sahel.* Ph.D. Thesis, The University of Edinburgh, U.K., 191 p.

Smith, D.M. and Allen, S.J. (1996). Measurement of sap flow in plant stems. Journal of Experimental Botany, 47, 1833-1844.

Smith, D.M., Jackson, N.A., Roberts, J.M. and Wallace, J.S. (1996). *Root Quantity, Activity and Below-Ground Competition in Grevillea robusta Agroforestry Systems*. Annual Report to the ODA Forestry Research Programme, Institute of Hydrology, Wallingford, U.K., 19 p.

Smith, D.M., Jarvis, P.G. and Odongo, J.C.W. (1997). Energy budgets of windbreak canopies in the Sahel. Agricultural and Forest Meteorology, **86**, 33-49.

Soegaard, H. and Boegh, E. (1995). Estimation of evapotranspiration from a millet crop in the Sahel combining sap flow, leaf area index and eddy correlation technique. Journal of Hydrology, **166**, 265-282.

Spiers, N. and Stewart, M. (1992). Uses of Grevillea robusta in Embu and Meru districts of Kenya. In: *Grevillea robusta in Agroforestry Systems*. Harwood, C.E. (ed.). ICRAF, Nairobi. pp 37-48.

Squire, G.R. (1990). *The Physiology of Tropical Crop Production.* CAB International, Wallingford, U.K., 236 p.

Steele, W.M., Allen, D.J. and Summerfield, R.J. (1985). Cowpea (*Vigna unguiculata* (L.) Walp.). In: *Grain Legume Crops*. Summerfield, R.J. and Roberts, E.H. (eds.). Collins, London., pp 520-583.

Stigter, C.J. and Baldy, C. (1995). Manipulation of the microclimate by intercropping: Making the best use of services rendered. In: *The Ecophysiology of Tropical Intercropping*. Sinoquet, H. and Cruz, P. (eds.). INRA Editions, Paris.

Stirling, C.M., Williams, J.H., Black, C.R. and Ong, C.K. (1990). The effect of timing of shade on development, dry matter production and light use efficiency in groundnut (*Arachis hypogaea* L.) under field conditions. Australian Journal of Agricultural Research, **41**, 633-644.

Summerfield, R.J., Huxley, P.A. and Steele, W.M. (1974). Cowpea (*Vigna unguiculata* (L.) Walp.). Field Crop Abstracts, **27**, 301-312.

Summerfield, R.J., Pate, J.S., Roberts, E.H. and Wein, H.C. (1985). The physiology of cowpea. In: *Cowpea: Research, Production and Utilisation.* Singh, S.R. and Rachie, K.O. (eds.). Wiley, New York., pp 65-101.

Swallow, B.M. (1995). *Economics of Dryland Degradation and Restoration: An African Perspective.* Presented at the International Workshop on Combatting Global Warming by Combatting Land Degradation, Nairobi, September 4-8.

Thapa, B. (1994). *Farmers' Ecological Knowledge About the Management and Use of Farmland Tree Fodder Resources in the Mid-Hills of Eastern Nepal.* PhD. Thesis, University of Wales, Bangor, U.K.

Thapa, B., Sinclair, F.L. and Walker, D.H. (1995). Incorporation of indiginous knowledge and perspectives in agroforestry development. II. Case study on the explicit representation of farmers' knowledge. Agroforestry Systems, **30**, 277-294.

Thimma Raju, K.R. (1992). Silver oak (*Grevillea robusta*) a multipurpose tree for arid and semi-arid regions. In: *Grevillea robusta in Agroforestry Systems.* Harwood, C.E. (ed.). ICRAF, Nairobi.

Thomas S.M., Whitehead, D., Adams, J.A., Reid, J.B., Sherlock, R.R. and Leckie, A.C. (1996). Seasonal root distribution and soil surface carbon fluxes for one-year old *Pinus radiata* trees growing at ambient and elevated carbon-dioxide concentration. Tree Physiology, 16, 1015-1021.

Thorburn, P.J., Hatton, T.J. and Walker, G.R. (1993). Combining measurements of transpiration and stable isotopes of water to determine ground water discharge from forests. Journal of Hydrology, **150**, 589-614.

Thottappilly, G. and Russell, H.W. (1985). World wide occurrence and distribution of virus diseases. In: *Cowpea: Research, Production and Utilisation.* Singh, S.R. and Rachie, K.O. (eds.). Wiley, New York.

Tournebize, R., Sinoquet, H. and Bussiere, F. (1996). Modelling evapotranspiration partitioning in a shrub/grass alley crop. Agricultural and Forest Meteorology, **81**, 255-272.

Tyndall, B. (1993). *Economic Evaluation of Grevillea Boundary Trees Planted Next to Maize and Beans in UM4 Kirinyaga.* KARI/KEFRI/ICRAF report.

Valentine, H.T. (1985). Tree-growth models - derivations employing the pipe-model theory. Journal of Theoretical Biology, **117**, 579-585.

van den Beldt, R.J. (1990). Agroforestry in the semi-arid tropics. In: *Agroforestry: Classification and Management.* MacDicken, K.G. and Vergara, N.T. (eds.). John Wiley and Sons, New York, pp 150-194.

van den Beldt, R.J. and Williams, J.H. (1992). The effect of soil surface temperature on the growth of millet in relation to the effect of *Faidherbia albida* trees. Agricultural and Forest Meteorology, **60**, 93-100.

Vandermeer, J. (1989). *The Ecology of Intercropping.* Cambridge University Press, Cambridge, UK.

van Noordwijk, M., Widianto, Heinen, M. and Hairiah, K. (1993). Old tree root channels in acid soils in the humid tropics: Importance for root penetration, water infiltration and nitrogen management. Plant and Soil, **134**, 37-44.

Visser, T. (1960). Interplanting in tea. I. Effects of shade trees, weeds and bush crops. Tea Quarterly, **32**, 69-87.

Walker, J.M. (1970). Effects of alternating versus constant soil temperature on maize seedling growth. Soil Science Society of America Proceedings, **34**, 889-892.

Wallace, J.S. (1991). The measurement and modelling of evaporation from semi-arid land. In: *Soil Water Balance in the Sudano-Sahelian Zone. Proceedings of Niamey Workshop, 1991.* Sivakumar, M.N.K., Wallace, J.S., Renard, C. and Giroux, C. (eds.). IAHS Publication No. 199, pp 131-148.

Wallace, J.S. (1996). The water balance of mixed tree-crop systems. In: *Tree-Crop Interactions: A Physiological Approach.* Ong, C.K. and Huxley, P. (eds.). CAB International, U.K., pp 189-234.

Wallace, J.S. and Batchelor, C.H. (1996). Managing water resources for crop production. In: *Land Resources: On the Edge of a Malthusian Precipice.* Greenland, D.J., Gregory, P.J. and Nye, P.H. (eds.). Royal Society, CAB International, Wallingford, Oxon, U.K., pp 77-87.

Wallace, J.S., Batchelor, C.H., Dabeesing, D.N., Teeluck, M. and Soopramanien, G.C. (1991). A comparison of the light interception and water use of plant and first ratoon sugar cane intercropped with maize. Agricultural and Forest Meteorology, **57**, 85-105.

Wallace, J.S., Lloyd, C.R. and Sivakumar, M.V.K. (1993). Measurements of soil, plant and total evaporation from millet in Niger. Agricultural and Forest Meteorology, **63**, 149-169.

Wallace, J.S., Jackson, N.A. and Ong, C.K. (1995). *Water Balance of Agroforestry Systems on Hillslopes.* Final Report to ODA Forestry Research Programme, Report No. 95/10, Institute of Hydrology, Wallingford, 39 p.

Waring, R.H., Schroeder, P.E. and Oren, R. (1982). Application of the pipe model-theory to predict canopy leaf-area. Canadian Journal of Forest Research, **12**, 556-560.

Warrington, I.J. and Kanemasu, E.T. (1983). Corn growth response to temperature and photoperiod. 1. Seedling emergence, tassel initiation and anthesis. Agronomy Journal, **75**, 744-754.

Wein, H.C. and Summerfield, R.J. (1984). Cowpea (*Vigna unguiculata* (L.) Walp.). In: *The Physiology of Tropical Field Crops.* Goldsworthy, P.R. and Fisher, N.M. (eds.). John Wiley and Sons, Chichester, U.K., pp 353-383.

Wenger, K.F. (1952). Effect of moisture supply and soil texture on the growth of sweetgum and pine seedlings. Journal of Forestry, **50**, 864.

Werk, K.S., Oren, R., Schulze, E.-D., Zimmermann, R. and Meyer, J. (1988). Performance of Two *Picea abies* (L.) Karst. stands at different stages of decline. III. Canopy transpiration of green trees. Oecologia, **76**, 519-524.

Whittaker, R.H. and Marks, P.L. (1975). Methods of assessing terrestrial productivity. In: *Primary Production in the Biosphere.* Leith, H. and Whittaker, R.H. (eds.). Springer-Verlag, New York, pp 105-118.

Willey, R.W. (1985). Evaluation and presentation of intercropping advantages. Experimental Agriculture, **21**, 119-133.

Williams, K.E. (1997). *On-Farm Evaluation of the Performance and Adoption of Agroforestry Systems in the Machakos District, Kenya.* BSc. Hons Thesis, The University of Nottingham, U.K.

Yobterik, A.C., Timmer, V.R. and Gordon, A.M. (1994). Screening agroforestry tree mulches for corn growth: A combined soil test, pot trial and plant analysis approach. Agroforestry Systems, **25**, 153-166.

Young, A. (1989). *Agroforestry for Soil Conservation. Science and Practice of Agroforestry 4.* CAB/ICRAF, Oxon, UK.

Zahner, R. (1962). Terminal growth and wood formation by juvenile loblolly pine under two soil moisture regimes. Forest Science, **8**, 345.

Zahner, R. (1968). Water deficits and the growth of trees. In: *Water Deficits and Plant Growth Vol. II Plant Water Consumption and Response.* Kozlowski, T.T. (ed.). Academic Press, New York and London, pp 191-254.

Zhang, Y.J., Hou, W,H., and Hou, Y.X. (1988). Ecological and physiological characteristics of several dune-fixing shrubs and trees in the Min-Qin district in Gansu Province. Chinese Journal of Arid Land Research, **1**, 323-333.